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GENETICS

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GENETICS

AN INTRODUCTION TO THE STUDY OF HEREDITY

BY

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Third Edition

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TO THE MEMORY OF

MY MOTHER

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PREFACE TO THE THIRD EDITION

This book refuses to stay finished, hence after seventeen years a second revision is necessary.

In some fields of human endeavor for which text-books are written, the subject matter may quite suitably be presented in a form comparable to isolated pictures, but the only way to treat correspondingly the kaleidoscopic subject of modern *Genetics* would be to resort to a moving picture apparatus, because the extensions of genetical knowledge are being made so rapidly that even text-book summaries of it demand continuous modification and realignment.

The pioneers in Genetics are for the most part not yet historical personages but are still present with us in flesh and blood, so that the student who would study the problems of heredity today can feel all the exhilaration and joy that comes with working at dawn while the day is yet fresh.

On the theoretical side of Genetics within the present generation much of the nature and origin of the germinal determiners has been made out. It is known, for instance, that they are independent enough to be separable at the time of maturation, and transferable in hybridization; that environmental factors, external or internal, may under certain circumstances directly affect them, but that the somatic envelope which encloses the germinal determiners exercises little or no modifying influence upon them.

Probably the surest advance and the greatest conquests in heredity are being made along theoretical rather than so-called

practical lines. Nevertheless the lure of possible rewards to be gained from the practical application of newly found genetical facts to the cultivation of plant crops and to the improvement of domestic animals, remains a very great incentive to man, although it must be acknowledged that the exaggerated and baseless hopes accompanying the first flush of the Mendelian renaissance have begun to give way to the more prosaic period of patient and persistent hard work inevitably necessitated in overcoming unforeseen obstacles to complete success which have arisen in the course of applying the new knowledge.

The incentive to continued effort, even in the face of possible failure, still remains. If by manipulating in any way hereditary genes it is possible to add only a single kernel to the average ear of corn, the potential gain in the United States alone where corn is the principal crop would easily become a matter of millions of dollars. Or in the same way if in the light of genetical knowledge the wheat crop could be made to ripen on even a single day earlier the resulting conquest in available wheat-producing area would be enormous.

Eugenics, or the application of genetical laws to man, is emerging out of the obscuring fogs of speculation and opinion into the light of day as an organized body of substantiated knowledge. In this field of easy prejudices the last word is far from being said. In fact at present the popular impression is general that everyone is talking at once, but nevertheless unmistakable advance is being made.

Again, the whole subject of sex, which has been a perennial center of interest for mankind from time immemorial, is proving to be a scientific gold mine to the geneticist who is supposed to approach its theoretical aspects with a cold, unromantic eye.

To meet these new advances in the practice and theory of the fundamental laws of Genetics, it has been found necessary to overhaul thoroughly the presentation of the subject in this book. Nearly every page has been modified, consequently, in some particulars, and considerable additional matter has been supplied, in the hope that the circle of friends who have found the book useful in the past may be retained and enlarged.

H. E. W.

PROVIDENCE, R. I.
March, 1930.

PREFACE TO THE FIRST EDITION

The following pages had their origin in a course of lectures upon Heredity, given at Brown University during the winter of 1911-1912, which were amplified and repeated in part the following summer at Cold Spring Harbor, Long Island, before the biological summer school of the Brooklyn Institute of Arts and Sciences.

An attempt has been made to summarize for the intelligent, but uninitiated, reader some of the more recent phases of the questions of heredity which are at present agitating the biological world. It is hoped that this summary will not only be of interest to the general reader, but that it will also be of service in college courses dealing with evolution and heredity.

The subject of heredity concerns every one, but many of those who wish to become better informed regarding it are either too busily engaged or lack the opportunity to study the matter out for themselves. The recent literature in this field is already very large, with every indication that much more is about to follow, which is a further discouragement to non-technical readers.

It may not be a thankless task, therefore, out of the jargon of many tongues to raise a single voice which shall attempt to tell the tale of heredity. There may be a certain advantage in having as spokesman one who is not at present immersed in the arduous technical investigations that are making the tale worth telling. The difficulties in understanding this com-

plicated subject may possibly be realized better by one who is himself still struggling with them, than by the seasoned expert who has long since forgotten that such difficulties exist.

Among others I am particularly indebted to Dr. C. B. Davenport for many helpful suggestions, to my colleague, Professor A. D. Mead, for reading the manuscript critically, to Dr. S. I. Kornhauser who gave valuable aid in connection with the chapter on the Determination of Sex, and to my wife for assistance in final preparation for the press.

I wish to thank Professor H. S. Jennings and Dr. H. H. Goddard, who have given generous permission to copy diagrams, as well as The Outlook Company and The Macmillan Company for the use of figures 24 and 66, respectively.

The fact that not all the suggestions which were at various times offered by my kindly critics have been incorporated in the text, absolves them from responsibility for whatever remains.

H. E. W.

PROVIDENCE, R. I.
September, 1912.

PREFACE TO THE REVISED EDITION

Nearly ten years have passed since this book first appeared. The biological Rip van Winkle of today who, awaking after a decade of somnolence, gazes again upon the genetic village of Falling Waters, will indeed need to rub his astonished eyes at the changed scene that now spreads out before him. Many old familiar landmarks, such as "unit characters" and "dominance," show signs of dilapidation, while strange children, shouting a medley of outlandish words, "linkage," "tetraploidy," and "non-disjunction," for example, are playing new games on the village green.

Although the remarkable advances in this field of science are well treated in considerable detail by several recent textbooks, notably those of Castle, Morgan, Conklin, and Babcock and Clausen, perhaps there still remains the original need for a more elementary presentation of the salient points of genetics, not only for the interested but confused layman, but also for the initiation of the prospective student who is attracted to the study of heredity.

To perform this service is the ambitious object of the present revision.

Three new chapters, XI, XII and XIII, have been added and the whole book has been thoroughly worked over and rearranged. Chapter XIII upon Sex Determination has practically been written by Professor S. I. Kornhauser of Denison University and the entire manuscript critically read by Dr. J. W. Wilson of Brown University.

There are thirty-four new figures and diagrams which are either original or copied from acknowledged sources. Mr. C. J. Fish made the drawings for figures 22 and 32. The proof was read by my wife and by my niece, Miss Dorothy Walter.

I wish to acknowledge the help I have received from all of these sources as well as from many unnamed friends who have given valuable suggestions.

H. E. W.

La Jolla, Calif.
March, 18, 1922.

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CHAPTER I

INTRODUCTION

1. The Idea of Species

The doctors have always disagreed regarding a definition of species. What determines the exclusive boundaries that shall isolate from their fellows any particular group of animals or plants has long been a mooted question, and still remains so, but in any case the peculiarities of structure upon which a species is based are a matter of heredity.

The Linnæan concept of a species was that of an exclusive caste of individuals, inflexibly demarked, over whose high barriers no nondescript tramps would dare attempt to climb. When an entomologist of the old Linnæan school encountered an insect which did not conform to the morphological traditions of its fellows, the frequent fate of such a nonconformist was to perish under the boot-heel rather than to find sanctuary in the cabinet of the preserved. Since it was an exception, and a violator of the divine law of the fixity of species, it deserved to be annihilated! Those were hard days both for heretics and for variations.

The method of the older school of systematists may be described as one which emphasized *differences* and put up barriers that should keep the unlike apart, at the same time allowing only "birds of a feather" to flock together. It was a brave and successful attempt to bring order out of chaos by classifying the living world, and it served its purpose well

until more than a half century ago when Darwin's idea that the origin of all species is from preceding species put an entirely new face upon the whole matter. Organisms of different species were then assumed to be *related to one another,* and even man could no longer escape acknowledging his poor animal relations. As a consequence, *likenesses rather than differences* thereafter claimed the most attention.

During the reconstruction of phylogenetic trees, which seized the imagination and became the principal business of post-Darwinian biologists, "connecting links," that is, the crotched sticks in the woodpile of organisms, which had hitherto been largely discarded, were most eagerly sought after. It was just these scraggly sticks, that were neither entirely trunk nor limb-wood but combinations of both, which told the story of continuity and were indispensable in building up a reunited whole. It was realized that the cautious advice of Bateson to "Treasure your exceptions" was sound advice.

As the analysis of the living world was gradually shifted from species to individuals, it was shown that individuals may be regarded simply as aggregates of *unit characters* which may combine so variously that it becomes more and more difficult to maintain constant limits of any kind between the groups of individuals arbitrarily called "species."

2. The Triangle of Life

Accordingly within a generation the center of biological interest gradually swung from the origin of species to the origin of the individual. The nineteenth century was Darwin's century. His monumental work "On the Origin of Species by Means of Natural Selection," which appeared in 1859, not only dominated the biological sciences but also in-

fluenced profoundly many other realms of thought, particularly those of philosophy and theology.

Now, in the first decades of the twentieth century, a particular emphasis is being laid upon the study of heredity, which is concerned with the perpetuation rather than the origin of species. The interpretation of investigations along this line of research has been made possible through the cumulative discoveries of many things that were not known in Darwin's day. Trained students, patiently and persistently bending over improved microscopes, have untangled many of the mysteries of the cell, while an increasing host of investigators, inspired by the Austrian monk Mendel, have industriously devoted their energies to the experimental breeding of animals and plants with an insight denied to investigators of preceding centuries.

The study of the origin of the individual, which has grown out of the more general consideration of the origin of species, forms the subject-matter of heredity, or, to use the more definitive word of Bateson, of *genetics*.

It is not with the individual as a whole that genetics is chiefly concerned, but rather with *characteristics* that make up the individual.

Three factors acting together determine the characteristics of an individual, namely, *environment, response,* and *heritage,* as expressed diagrammatically in Figure 1. It may be said that an individual is the result of the *interaction* of these three factors since he may be modified by changing any one of them. Although no one factor can possibly be omitted, the student of genetics places the emphasis upon heritage as the factor of greatest importance. Heritage, or "blood," expresses the innate equipment of the individual. It is what he actually *is* even before birth. It is his nature. It is what determines

whether he shall be a beast or a man. Consequently in the diagram (Fig. 1), the triangle of life is represented as resting solidly upon the side marked "heritage" for its foundation.

Environment and response, although indispensable, are both factors which are subsequent and secondary. Environment is what the individual *has,* for example, housing, food, friends and enemies, or surrounding aids which may help him and obstacles which he must overcome. It is the particular world

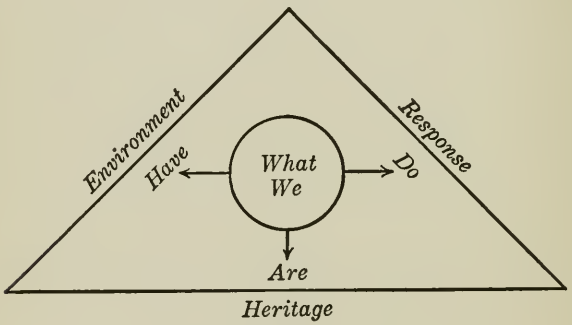

Fig. 1.—The triangle of life.

into which he comes, the measure of opportunity given to his particular heritage. Lacking a suitable environment a good heritage may come to naught like good seed sown upon stony ground, but it is nevertheless true that the best environment cannot make up for defective heritage or develop wheat from tares.

Response, on the other hand, represents what the individual *does* with his heritage and environment. It is what may be described as the training or educational factor, most clearly demonstrable in the higher animal forms.

The absence of sufficient response even when the environment is suitable and the endowment of inheritance is ample

will result in an individual who falls short of his possibilities, while no amount of response or education can develop a man out of the heritage of a beast. "What a man *can* do is prescribed by heredity, what he *does* is determined by circumstance" (Cattell). Consequently the biologist holds that, although what an individual *has* and *does* is unquestionably of great importance, particularly to the individual himself, what he *is* in the long run is far more important. Improved environment and training may better the generation that is already born. Improved blood will better every generation to come.

As far as the individual is concerned, since he has no part in selecting his parents, through whom his inheritance comes, there is no real ground for the pride in "good blood," that is sometimes rather flamboyantly displayed. If one is well-born, he may properly be glad and rejoice in his good fortune, but the only valid excuse for pride is the consciousness of having made the best of whatever equipment one has in the environment in which he finds himself.

The "triangle of life," when applied to man, shows that there are theoretically at least a minimum of twenty-seven possible kinds of human beings, as shown in Figure 2. Climbing up this "scale of success" is what makes life worth living. It is illuminating for anyone to determine judiciously where he himself stands at present, or to assign places mentally to various other people, historical or contemporary, in this scale.

The left-hand factor does not change throughout life but the other two may. The sociologist and the philanthropist are immediately concerned with the middle column; the educator and particularly the parent and one's self with the right-hand column; while the biologist puts faith in the left-hand column of "heritage." For example, a child born AZZ is more

	Heritage Environment Response
1.	A A A
2.	A A M
3.	A A Z
4.	A M A
5.	A M M
6.	A M Z
7.	A Z A
8.	A Z M
9.	A Z Z
10.	M A A
11.	M A M
12.	M A Z
13.	M M A
14.	M M M
15.	M M Z
16.	M Z A
17.	M Z M
18.	M Z Z
19.	Z A A
20.	Z A M
21.	Z A Z
22.	Z M A
23.	Z M M
24.	Z M Z
25.	Z Z A
26.	Z Z M
27.	Z Z Z

FIG. 2.—The scale of success. A stands for high grade; M, for mediocrity; Z, for low grade.

apt to reach the top than one born ZZZ. In selecting a mate it would be far wiser to marry AZZ than ZAA, since "blood will tell." Obviously twenty-seven kinds of men fall far short of the actual variety, for no two are exactly alike. The median grade of M represents but a small part of the possible range of variety between the theoretical extremes of A and Z.

What, then, is this "blood" or heritage? Exactly what is meant by heredity?

3. A Definition of Heredity

The terms *heredity* and *inheritance* come to us from legal usage. We "inherit" the old homestead or our grandfather's clock. Moreover, as "heirs to all the ages" our heredity includes everything that goes to make up civilization, such as the arts, sciences, literature and traditions. With this kind of heredity which is very evident and plays an unmistakably important rôle in determining what we have today we are not here concerned, for this is not what is meant by biological heredity.

Professor Castle, in his book on "Heredity in Relation to Evolution and Animal Breeding," has defined

heredity as "organic resemblance based on descent." The son resembles his father because he is a "chip off the old block." It would be still nearer the truth to say that the son resembles his father because they are *both chips from the same block,* since the actual characters of parents are never transmitted to their offspring in the same way that real estate or personal property is passed on from one generation to another. When, for example, the son is said to have his father's hair and his mother's complexion it does not mean that paternal baldness and a vanishing maternal complexion, are the inevitable consequences.

Biological inheritance is more comparable to the handing down from father to son of some valuable patent right or manufacturing plant by means of which the son, in due course of time, may develop an independent fortune of his own, resembling in character and extent the parental fortune similarly derived although not identical with it.

So it comes about that "organic resemblance" between father and son, as well as that which often appears between nephew and uncle or even more remote relatives, is due not to a direct entail of the characteristics in question, but to the fact that the characteristics are "based on descent" *from a common source.*

In other words, an "hereditary characteristic" of any kind is not an entity or unit which is handed down from generation to generation, but is rather a *method of reaction* of the organism to the constellation of external environmental factors under which the organism lives. That is, it is the ability to respond in a definite similar way under similar conditions. Blood agglutination tests demonstrate, however, that similarity in appearance is not always a safe criterion of relationship, just as things of a kind collected together on

the shelves of a museum are not necessarily derived from a common source.

To unravel the golden threads of inheritance which have bound us all together in the past, as well as to learn how to weave upon the loom of the future not only those old patterns in plants and animals and men which have already proven worth while, but also new organic designs of an excellence hitherto impossible or undreamed of, is the inspiring task before the geneticist to-day.

4. The Maintenance of Life

So far as we know, every living thing on the earth to-day has arisen from some preceding form of life.

How the first spark of life began will probably always be a matter of pure speculation. Whether the beginnings of what is called life came through space from other worlds on meteoric wings, as Lord Kelvin has suggested; whether it was spontaneously generated on the spot out of lifeless components; or whether life itself was the original condition of matter, and the one thing that must be explained is not the origin of life but of the non-living, no one can say. Leaving aside the first speculation as untenable and the third as irrational, since it jars so sadly with what astronomers tell us of the probable evolution of worlds, the theory of spontaneous generation seems to be the last resort to which to turn.

In prescientific days this idea of spontaneous generation presented no great difficulties to our imaginative and credulous ancestors. John Milton, with the assurance of an eyewitness, thus described the inorganic origin of a lion:

> "The grassy clods now calved; now half appears
> The tawny lion, pawing to get free

His hinder parts—then springs as broke from bonds,
And rampant shakes his brindled mane."
("Paradise Lost," Book VII, line 543.)

Ovid also in his "Metamorphoses," not to mention any more familiar accounts of special creation, easily succeeded in creating mankind from the humble stones tossed by the juggling hands of Deucalion and Pyrrha.

Although under former conditions on the earth it might have been possible for life to have originated spontaneously, and although it may yet be possible to produce life from inorganic materials in the laboratory or elsewhere, the exhaustive work of Pasteur, Tyndall, and others effectually demonstrated more than a generation ago that living matter apparently always arises from preceding living matter, and this conclusion is generally accepted as an axiom in genetics.

There are various methods of producing *more* life, given a nest-egg of living substance with which to start. Any organism, whether plant or animal, is continually transforming inorganic and dead material into living tissue. Through the process of repair, for example, an injury to a form as highly developed even as man is frequently made good, as, for example, in the case of a skin wound, if it is not too extensive and does not involve too highly specialized tissues.

When the intake of non-living material is in excess of the outgo, growth results, with the consequence that more living substance is built up than existed before. Thus a fragment of a living sponge or a piece of a begonia leaf is sufficient to restore a duplicate of the original organism.

A process similar to the repair of the begonia leaf is that employed so effectively in the great groups of the one-celled animals and plants, the Protozoa and Protophyta, by means of which their numbers are maintained. These one-celled

organisms usually multiply by fission, that is, by division into halves, and each half then grows to the size of the parent organism from which it sprang. When two daughter protozoans are thus formed, they are essentially orphans because they have no parents, alive or dead. The parental substance in such a process, along with the regulating power necessary to reorganization and growth, goes over bodily into the next generation in the formation of daughter-cells, leaving usually no remains whatever behind. In primitive forms of this description, continuous life is the natural order, and death, when it does occur, is, as Weismann (1834-1914) has pointed out, accidental and quite outside the plan of nature.

In these cases, it is easy to see the reason for "organic resemblance" between successive generations. Parent and offspring are successive manifestations of the *same thing,* just as the begonia plant, restored from a fragment of a begonia leaf, is simply an extension of the original plant.

Many modifications of the process of multiplication by fission occur, all of them, however, agreeing in the fundamental principle that the progeny resemble the parents because they are pieces of the parents.

Thus the "greening" apple maintains its individuality although coming from thousands of different trees in various localities, because all of these trees through the asexual process of grafting are continuations of the one original Rhode Island greening tree grown by Dr. Solomon Downe in the town of Foster, over a century ago. Western navel oranges all come, directly or indirectly, from parts of one tree found near Bahia in Brazil. Most fruit trees and our various named varieties of roses, tulips, dahlias, potatoes, and many other plants, are kept true to type by processes either of budding, grafting, propagating by cuttings, or by other vegetative means, such as

bulbs, roots, and tubers, all of which are devices for preserving organic continuity.

Again, certain fresh-water sponges and bryozoans, quite unlike most of their marine relatives, keep a foothold from year to year within their particular shallow fresh-water habitats by isolating well protected fragments of themselves in the form of either *gemmules* or *statoblasts*. These structures may drop to the muddy bottom and live in a dormant condition throughout the icy winter when it would not be possible for the entire organism to survive near the surface.

In order to meet the conditions imposed by winter, however, these fragments have become so modified as temporarily to lose their likeness to the parent generation, although readily regaining that likeness when springtime brings the opportunity. The unity of two succeeding generations, notwithstanding that it may be interrupted by the temporary interposition of something apparently different in the form of gemmules or statoblasts, is thus essentially maintained. The bryozoan colonies of two successive seasons in a fresh-water pond may be regarded as parts of the same identical colony, since they present an "organic resemblance based on descent," although the sole representatives of the parent colony during midwinter may be the sparks of life locked up within the statoblasts buried in the mud.

Similarly, the asexual spores of many plants, such as molds, mosses and ferns, may be regarded as gemmules reduced to the lowest terms, namely, to single cells. As in the preceding cases, so in this instance the resemblance of the offspring which may arise from these spores to the parents which produced them is due to the essential material identity of two generations.

These illustrations of heredity in its simplest manifestations

give the key to "organic resemblance" higher up in the scale. Sexual reproduction is no less plainly the direct continuation of life, though in this instance *two* sporelike fragments out of one generation contribute to form the new individual of the next generation instead of *one* fragment. In all cases there is a *material continuity between succeeding generations.* Offspring become thus an extension of a single parent, or of two parents, while heredity is simply "organic resemblance based on descent."

5. Somatoplasm and Germplasm

In forms that reproduce sexually there occurs a differentiation of the living substance into what Weismann terms *somatoplasm* and *germplasm.*

Somatoplasm includes the body tissues, that is, the bulk of the individual, which is fated in the ordinary course of events to complete a life-cycle and die. Germplasm, on the contrary, is the immortal fragment freighted with the power to duplicate the whole organism and which, barring accident, is destined to live on and give rise to new individuals.

Germplasm thus carries potencies for developing more of both germplasm and somatoplasm, while somatoplasm, according to this conception, has only the power to repair itself and not to reproduce a new individual. Moreover, germplasm is not freshly formed in each generation, neither does it arise anew when the individual reaches sexual maturity, as it appears to do, but it is a continuous substance which is present from the beginning although it is periodic in its activities. In spite of the fact that this theory of the *continuity of the germplasm* has been actually demonstrated in comparatively few instances, all the facts we know concerning the behavior of the germinal substance are consistent with it. The success-

ful experiments of Carrel, Harrison, and others with isolated tissues grown for years *in vitro* would suggest that potential immortality is present at least in some somatic cells as well as in germplasm.

The phrase "life everlasting" is not confined, therefore, to the vocabulary of the theologian, for potential immortality is more than a mystical hope of believing humanity, since it is based upon demonstrable biological facts.

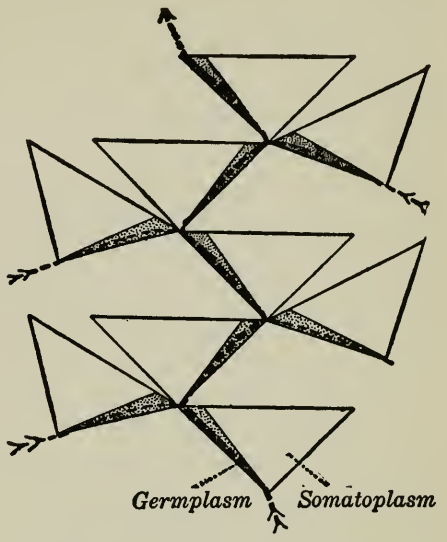

FIG. 3.—Scheme to illustrate *the continuity of the germplasm*. Each triangle represents an individual made up of *germplasm* (shaded) and *somatoplasm* (unshaded). The beginning of the life cycle of each individual is represented at the inverted apex of the triangle where germplasm and somatoplasm are both present. As the individual develops each of these component parts increases. In sexual reproduction the germplasms of two individuals unite into a common stream to which the somatoplasm makes no contribution. The continuity of the germplasm is shown by the heavy broken line into which run collateral contributions from successive sexual reproductions.

In many of the Protozoa, the entire organism is possibly comparable to germplasm, but in all forms of life that are compounded of several cells the germplasm is probably set aside early in the development of the individual, and this remains undifferentiated, or in reserve, like a savings-bank account put by for a rainy day, while the somatoplasm is expended to meet the immediate demands of

the tissues that make up the individual. In one instance at least, according to Boveri (1863-1916), who has followed out cell-lineage in the nematode worm *Ascaris,* this splitting off or isolation of the germplasm occurs as early in the cleavage of the fertilized eggs as the sixteen-cell stage, when fifteen of the cells go to form the somatoplasm and the sixteenth is set aside as germplasm.

Thus there results a continuous stream of germplasm, receiving contributions from other germplasmal streams at the time of sexual reproduction, as shown diagrammatically in Figure 3, in which individuals are represented by triangles. From this continuous stream of germplasm there split off at successive intervals complexes of somatoplasm, or "individuals," which go so far on the road of specialization into tissues that the power to be "born again" is lost, and so after a time they die, while the germplasm, held in reserve, lives on.

This is what is meant by saying that a father and son owe their mutual resemblance to the fact that they are chips off the same block rather than by saying that the son is a chip off the paternal block. Both somatoplasms are developments *at different intervals* from the same continuous stream of germplasm instead of one somatoplasm, derived from a preceding one. As a matter of fact the germplasm from which the son arises is modified by the addition of a maternal contribution, so that father and son in reality hold the same relation to each other that half-brothers do.

So far as his body or his somatoplasm is concerned, the son is younger than his father but at the same time he is older than his father in his germplasm, because this continuous line of germinal potentiality has a span of a generation longer in the son than in the parents.

From the point of view of genetics, then, the real mission

of the somatoplasm, so marvelously differentiated into all the various forms that we call animals and plants, is simply to serve as a temporary domicile for the immortal germplasm which, like the Wandering Jew, is destined to reappear in successive reincarnations. Thus the parent becomes as it were the "trustee of the germplasm," but not the producer of the offspring, for the soma is after all only the mechanism through which a fertilized egg produces in due time another fertilized egg. As someone has pointed out, a hen does not produce another hen through the medium of an egg, but a hen is merely an egg's way of producing another egg.

In the light of these preliminary explanations it is plain that the most hopeful point of attack in the science of genetics must inevitably be the hidden germplasm which is the source, or point of departure in the formation of each new individual, rather than the conspicuous somatoplasm, which represents only the end stages of the hereditary processes.

This has not been the method of study in the past. The resemblances of the visible parent and offspring have usually been traced through succeeding generations instead of the character of their unseen germplasms. By following this old method, investigators have often been misled because the visible or apparent is not always the true index of what lies behind it. A gray and a white rabbit, for example, may produce some offspring that are entirely black, or two white-flowering sweet peas when crossed may sometimes produce purple blossoms. Consequently it is a great fallacy to affirm that always in heredity "like produces like," since the opposite is quite often the case.

The new heredity, embodied in the science of genetics, attempts to go deeper than the surface appearance of the somatoplasm. It aims to get at the source or origin of organ-

isms, that is, the *germplasm* which is the only connecting thread between succeeding generations of living forms from the "unbeginning past." It is concerned not so much with somatoplasm, which represents what the germplasm has done in the past, as with the germplasm itself and what it can do in the future.

CHAPTER II

VARIATION

1. The Most Invariable Thing in Nature

In the introductory chapter it was shown that "organic resemblance based on descent," by which is meant heredity, is due principally to the fact that offspring are material continuations of their parents and consequently may be expected to be like them. The fact that this is the case in the great majority of instances has given rise to the popular formula, "like produces like," as a rule of heredity.

But this formula by no means always fits the facts. Like often produces something apparently unlike. For instance, two brown-eyed parents may produce a blue-eyed child, although brown-eyed children are more usual from such a parentage. It is a common experience, indeed, for breeders of plants and animals to meet with continual difficulties in getting organisms to breed true.

On the other hand, it is exactly these variations which so constantly interfere with "breeding true" that furnish the sole foothold for improvement. If all organisms did breed strictly true, one generation could not stand on the shoulders of the preceding generation, and there could be no evolutionary advance.

The most invariable thing in nature is variation. This fact is at once the hope and the despair of the breeder who seeks

to hold fast to whatever he has found that is good and at the same time tries to find something better. Variation is a veritable Pandora's box and the chaos that would ensue if it were not confined within certain predictable limits can hardly be imagined. Obviously the entire subject of variation is intimately and inevitably bound up with any consideration of genetics, for when the reasons for the similarities and dissimilarities between succeeding generations are clear, then heredity can be explained.

2. The Universality of Variation

Much of the variation in nature is patent to the most casual observer, but it requires a trained eye to see the universal extent of many minor differences. A flock of sheep may all look alike to a passing stranger, but not to the man who tends them. A dozen blue violet plants from different localities might easily be identified by the amateur botanist as belonging to the same species when, to a specialist on the genus *Viola,* unmistakable differences would doubtless be clearly evident.

So-called "identical twins" constitute so marked an exception to the universal rule of variational difference that they challenge the attention at once, yet even here upon critical examination there appears some degree of variation.

The fact that every attempt at an intimate acquaintance with any group of organisms whatsoever invariably reveals previously unrecognized variations, indicates that variability is much more widespread in nature than is commonly believed.

The key to Japanese art, as pointed out by Dr. Nitobe, consists in faithfully copying nature. It is for this reason that the Japanese artist makes each object that he produces unique,

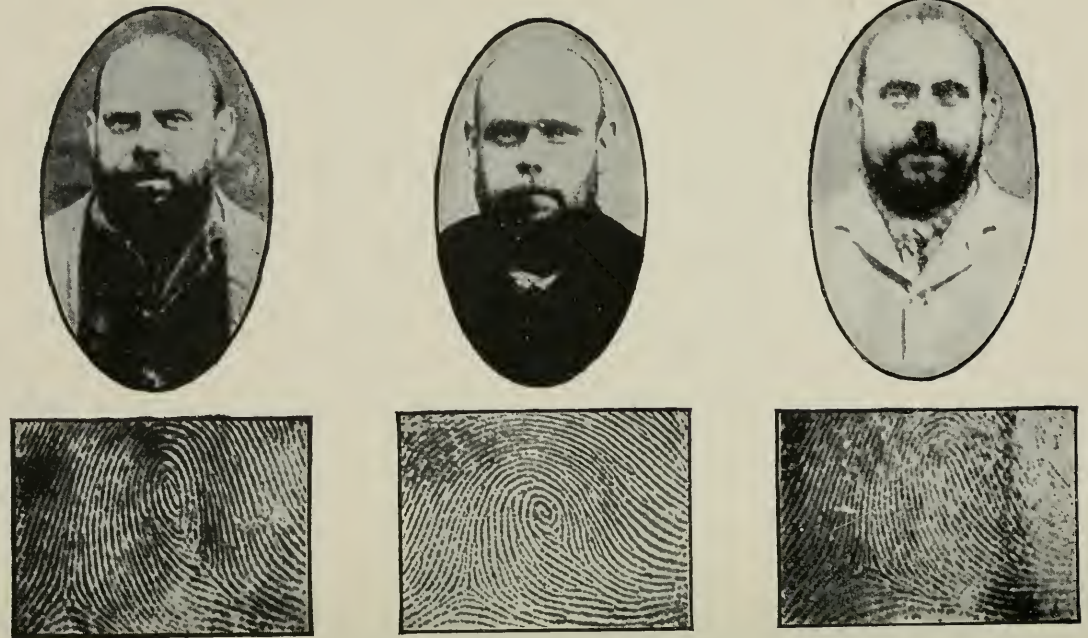

Fig. 4.—The constancy of minor variations. The thumb prints of these three criminals are characteristically different although their faces would easily confuse the ordinary observer. From *The Outlook* of Feb. 24, 1912.

because nature herself, whom he strives to follow, never duplicates anything.

The Bertillon system of personal identification is based upon the constancy of minor variations found in each individual. Its importance is shown in Figure 4. The faces of the criminals there pictured would be easily confused by the ordinary observer, but an examination of their thumb prints shows unmistakable differences between these three individuals.

On the other hand, over-emphasis upon the study and analysis of variation may tend to obscure the important fact that parent and offspring, in the vast majority of their characteristics, are alike.

3. Kinds of Variation

With respect to their nature variations may be morphological, physiological, or psychological. Under *morphological* variations are included differences in shape, size, and pattern as well as differences in number and relation of constituent parts.

Differences in activity are of *physiological* nature, as, for example, longevity, fecundity, immunity, degree of resistance to drought in plants or quality of milk production in cows. The kea parrot, after the introduction of sheep into New Zealand, changed from herbivorous to carnivorous habits, attacking and preying upon the sheep, and consequently became a pest. Many animals in captivity are less fertile than when free, while different individuals are well known to vary widely with respect to their susceptibility to disease. Nägeli reports the presence of tubercles in 97 per cent of the cases in five hundred human autopsies, although a majority of the deaths in question was not due to tuberculosis at all, a fact which indicates diversity in the resistance of different individuals to the tubercle bacillus.

Psychological variations in man, such as those which determine the temperament or mental traits of individuals, are apparent to everyone.

There are numerous other categories into which variations may be arranged, as, for example, whether they occur sporadically and singly or in multiple fashion; whether they are useful, indifferent, or harmful to the organism possessing them; whether they are orthogenetic or fortuitous in the manner of their historical appearance; whether they are continuous or discontinuous with relation to each other; whether they are qualitative or quantitative in character; and whether they are somatic or germinal in origin. In the present connection, however, the interest centers in variations with respect to their *heritability,* that is, whether they possess or lack the power to reappear in the following generation.

4. Methods of Studying Variations

Roughly stated, there are three ways of studying variations: *first,* Darwin's method of observation and description of more or less isolated cases; *second,* Galton's biometric method of statistical inquiry; and *third,* Mendel's experimental method. The second of these methods will be considered in this chapter.

5. Biometry

The science of biometry, that is, the application of statistical methods to biological facts, has been developed within recent years. Sir Francis Galton, Darwin's distinguished cousin, may be regarded as the pioneer in this field of research, while Karl Pearson and his disciples are representatives of the modern school of biometricians. Lord Kelvin once wrote, "I often say that when you can measure what you are speaking about and express it in numbers, you know some-

thing about it, but when you cannot measure it, when you cannot express it in numbers, your knowledge is of a meager and unsatisfactory kind; it may be the beginning of knowledge, but you have scarcely in your thoughts advanced to the stage of *science,* whatever the matter may be."

Although mathematical analysis of biological data when not sufficiently ballasted by biological analysis of the same facts may sometimes lead the investigator astray, yet often the only way to formulate certain truths or to analyze data of some kinds is by resort to statistical methods. Biometricians are quite right in insisting that it is frequently necessary to go further than the *fact* of variation, which may be apparent from the inspection of an individual case, and to deal with cumulative evidence as presented through statistical analysis.

In matters of heredity, however, variations as they occur in isolated cases and in definite pedigrees seem to offer a more hopeful line of approach than statistical generalizations involving many cases. It is better to become acquainted with the real parent than to evolve a hypothetical "mid-parent" mathematically. In this connection it is well always to bear in mind the warning of Johannsen, himself a past master in biometry, when he writes: *"Mit* Mathematik nicht *als* Mathematik treiben wir unsere Studien."

6. The Measurement of Variability

With respect to any measurable character there are bound to be deviations from an average condition. According to the mathematical laws of chance these deviations sometimes are plus and sometimes minus, and consequently they may be termed *fluctuating variations.*

Pearson gives as a simple illustration of fluctuating variation the number of ribs present in two sets of beech-leaves, as

shown below. These sets were taken at random from two different trees, and each contains twenty-six leaves.

Number of Ribs	13	14	15	16	17	18	19	20	Total
First tree . .			1	4	7	9	4	1	26
Second tree . .	3	4	9	8	2				26
Total . . .	3	4	10	12	9	9	4	1	

It will be seen that, while certain leaves might well belong to either tree, as, for example, those with sixteen ribs, the entire group of leaves from either tree is unlike that of the other tree. In the first instance the number of ribs fluctuates around eighteen as the commonest kind; in the second case, around fifteen. Such a difference, as may readily be seen, could not easily be detected or expressed by any other method than a statistical one.

Again, in a case of forty-seven starfishes all of which were collected from one locality the variation in the number of rays proved to be, according to Goldschmidt, an amount indicated graphically in Figure 5, where the data are arranged in the form of a so-called frequency polygon or curve.

From such a polygon certain *constants* may be computed which conveniently express in a single number, for purposes of abstract comparison, distinctions that otherwise could be handled only in the most indefinite way.

Thus in this instance the *arithmetical mean,* expressed by the hypothetical number 4.915, a number which of course does not actually occur in nature, is simply the average number of rays in the forty-seven starfishes selected at random.

The *mode* which represents the group containing the largest number of individuals of a kind, namely, thirty out of forty-seven, is five in this particular polygon. If all individ-

uals fell within the mode there would be no variation and the polygon would become a vertical line.

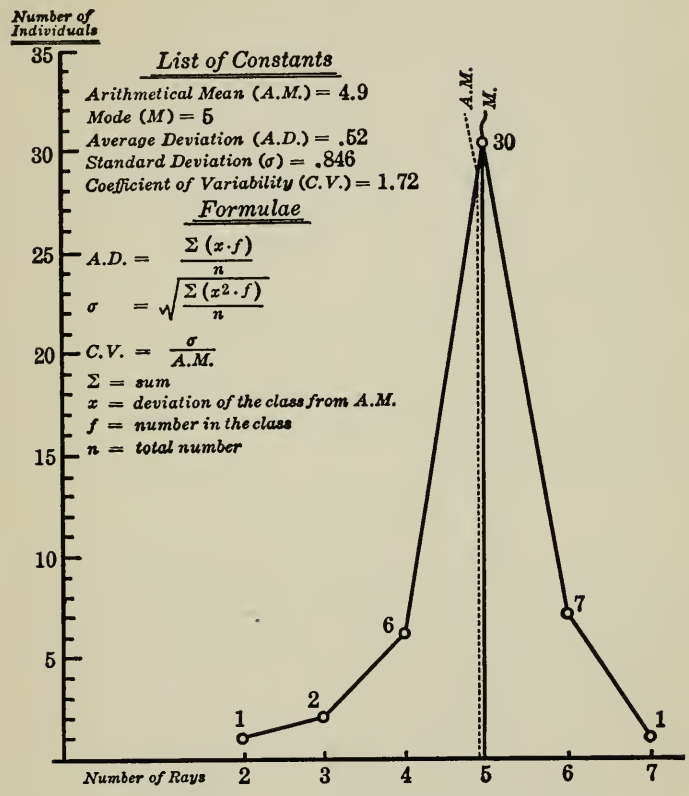

FIG. 5.—The fluctuating variability of starfish rays. From data by Goldschmidt.

The *average deviation,* which is an index of the amount of variation going on among the starfishes in question, is .52. In other words, .52 of a ray is the average amount that each individual starfish deviates from the arithmetical mean of 4.915. Although the one seven-rayed starfish which happens

to be in the lot varies from the standard of 4.915 to the extent of 2.085 (7—4.915) rays, there are thirty five-rayed starfishes which vary only .085 (5—4.915) of a ray, and consequently the average of the entire forty-seven amounts to .52 of a ray. In another collection of starfishes where either more seven-rayed or two-rayed specimens might be present, the average deviation would probably be greater.

By computing the average deviation, therefore, and using it as the criterion of variation, a comparison of the variability of organisms that have been taken from different localities or subjected to different conditions can be definitely expressed.

A measure of variability more commonly in use by biometricians, because of its relation to probable error, is the *standard deviation*. This is the square root of the sum of all the deviations squared and their frequencies divided by n, according to the formula

$$\sigma = \sqrt{\frac{\Sigma (x^2 \cdot f)}{n}}$$

in which x represents the deviation of each class from the arithmetical mean; f, the number of individuals in each separate class; Σ, the sum of the classes; and n, the total number of individuals.[1]

In the present instance the standard deviation is .846, a number that has valuable significance only when brought into comparison with standard deviations similarly derived from other groups of starfishes.

Such a variation polygon as the above expresses the law that the farther any single group is from the mean of all the groups making up the polygon, the fewer will be the individuals representing it.

[1] For directions explaining the use of such formulæ see Davenport's "Statistical Methods."

In computing the standard deviations the results will be less reliable from small than from large samples. It is customary, therefore, to safeguard the result by appending the *probable error,* in order to indicate the limits within which the conclusions are significant. By "probable error" is meant a measure of reliability indicating how far a calculation, based upon a limited sample of cases, may differ either plus or minus from the true theoretical value which would include all possible cases of the same category.

The formula for the probable error of standard deviation is

$$PE_\sigma = \pm \frac{0.6745 \times \sigma}{\sqrt{2n}}$$

and three times the probable error is arbitrarily considered as the limit by which two determinations may differ from one another and still be regarded as significant deviations from the true value. On page 26, for example, the standard deviation for *Urosalpinx* shells from Massachusetts, to be explained further in the next paragraph, is $2.335 \pm .0386$, while the corresponding figure for California shells of the same species is $3.138 \pm .0538$. Three times the probable error in the first case is .1098, consequently the limits of reliability lie between 2.4448 (2.335 + .1098) and 2.2252 (2.335 − .1098), while in the second case three times the probable error is .1614 and the limits fall between 3.2994 (3.138 + .1614) and 2.9766 (3.138 − .1614). The standard deviations of the Massachusetts and the California shells would, therefore, be considered as differing significantly from each other since the ranges of the two cases do not even overlap.

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7. The Interpretation of Variability Curves

a. Relative Variability

The statistical determination of the relative variability of two lots of organisms with respect to a certain character may be illustrated by the case of the oyster-borer snail, *Urosalpinx cinereus,* as seen in the accompanying table.

Atlantic and Pacific Shells Compared

Locality		Number of Shells	A.M.	σ	Probable Error
Woods Hole	West Shore	1,001	58.928	2.339	±.0352
	Penzance Point	1,002	61.718	2.737	±.0412
	Nobska Point	1,002	61.737	2.152	±.0324
	Nobska Point	1,001	61.944	2.234	±.0337
	Nobska Point	496	66.944	2.366	±.0507
	Barnacle Beach	998	63.932	2.604	±.0393
	Big Wepecket	1,006	57.426	2.052	±.0308
	Mid-Wepecket	500	57.606	2.098	±.0447
	Average for Mass.		61.066	2.335	±.0386
California	Belmont Beds	1,008	59.051	3.023	±.0454
	San Francisco Bay	520	60.892	3.361	±.0703
	Average for Cal.		59.664	3.138	±.0538
	Difference			.803	

The obvious conclusion to be drawn from this table is that the snails, which were unintentionally carried from the Atlantic coast to California in the transplantation of oysters, show more variation in their new habitat than they did in the old one with respect to the particular character measured, namely, the relative size of the mouth aperture compared with the height of the entire shell.[1]

[1] "Variation in Urosalpinx." Walter. Amer. Nat. 1910, Vol. XLIV, pp. 577-594.

Although a further analysis of the data in this particular case shows that this conclusion is probably biologically incorrect, this discovery does not invalidate it as an illustration of a mathematical method of determining relative variability.

b. Bimodal Polygons

Sometimes two conspicuous modes make their appearance in a frequency polygon, as Jennings found, for example, in meas-

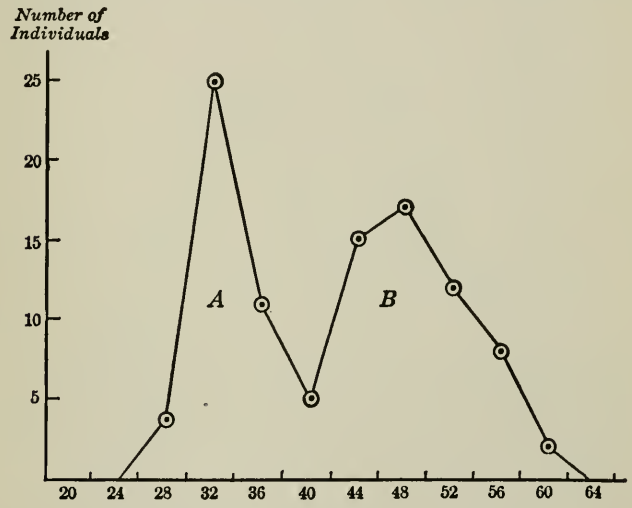

FIG. 6.—The body-width of a population of the protozoan *Paramecium*, showing a polygon with two modes. *A, Paramecium aurelia. B, Paramecium caudatum.* After Jennings.

uring the body-width of a population of the protozoan *Paramecium* (Fig. 6).

It was subsequently found that the two modes in this polygon were due to the fact that the material in question was a mixture of two closely related species, *Paramecium aurelia* and *Paramecium caudatum,* the individuals of which ar-

ranged themselves around their own mean in each instance according to expectation.

Although such an explanation does not always turn out to be the right one, the biometrician is led to suspect whenever a two or more moded polygon appears that he is dealing with a mixture of more than one kind of material, each of which fluctuates around its own average.

FIG. 7.—The ribs of leaves from two beech trees. When put together they form a polygon which does not reveal its double origin. From data by Pearson.

Heterogeneous material, it should be noted, does not always give a bimodal curve. For example, if Pearson's two lots of beech leaves mentioned above are mixed together, they form a regular series from the inspection of which no one could infer their double origin. (See the heavy line in Figure 7.)

c. Skew Curves

The direction in which variations are tending may sometimes be determined by the statistical method. As an illus-

tration of this may be cited the number of ray florets in 1000 white daisies (*Chrysanthemum leucanthemum*), 500 of which were collected at random by the writer from a small patch in a swampy meadow in northern Vermont, while the other

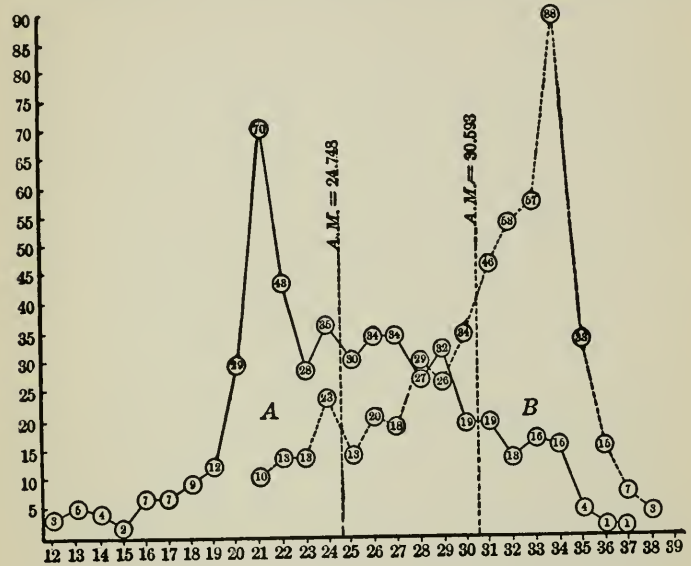

FIG. 8.—Variation in the ray florets of the white daisy (*Chrysanthemum leucanthemum*). *A*, from a swampy meadow. *B*, from a dry hillside pasture near by. Both the curves are "skew" because in each case there is an admixture of the other type. The distinction between the two types is due to heredity rather than to environment.

500 were selected in the same random manner upon the same day from a dry hillside pasture hardly more than a stone's throw distant. Among these two lots of daisies the number of ray florets varies from twelve to thirty-eight and their frequency polygons, as shown in Figure 8, form what are termed "skew curves," because the mode in each case lies considerably to one side of the arithmetical mean.

It will be seen that lot *A* from the swampy meadow, which in spite of the greater fertility of the soil and the unquestionably greater luxuriance of the plants themselves, produced heads with fewer florets, fluctuates around the number 21, while the dry pasture population *B,* characterized by blossoms which were in general noticeably smaller, fluctuates around the number 34. The habitats of the two lots were so near together, however, that there was probably a considerable intermixture of the two types, as shown by the tendency of each polygon to produce a second mode. Thus the *A* polygon shows that there is an increasing tendency or variability in the twenty-one floret type toward the thirty-four floret type, due probably in this particular instance to invasion resulting from the proximity of the *B* colony.

8. Correlation

Another application of biometry to the problems of heredity is the use of *correlation tables* and *coefficients of correlation,* to express the degree of resemblance between the members of successive generations as shown by measurable characteristics. The same methods are also employed to determine the amount of causal relationship between the two variable characteristics in organisms of a single generation. The interdependence of measurable variations is frequently difficult to ascertain by simple inspection of the data, and consequently the more exact methods of biometry have to be employed. Furthermore, computed correlations give definite numerical values which are readily comparable one to another. As an illustration of correlation may be cited data obtained by Hayes [1] on the relationship between the number of leaves and the

[1] "Correlation and Inheritance in *Nicotiana tabacum*." Conn. Agri. Exp. Sta., Bull. 171, 1912.

height of the plants of certain kinds of tobacco. Three sample correlation tables, with the coefficients of correlation computed from the same data, are given below.

In arranging these tables of correlation each plant is recorded horizontally for the number of its leaves, and vertically for its height in inches. The table is then divided into four quadrants by a horizontal line representing the *average number of leaves,* and by a vertical line representing the *average height* of all the plants. With reference to number of

TABLE 1

CORRELATION BETWEEN NUMBER OF LEAVES AND HEIGHT OF PLANT OF #401 "BROADLEAF" TOBACCO

Height of Plants in Inches \ Number of Leaves	17	18	19	20	21	22	
44				1			1
47		3	1				4
50		7	10	3			20
53	2	13	17	11	1		44
56	1	5	21	14	3	1	45
59		1	10	8	1	1	21
62		1	6	4	2	1	14
65						1	1
	3	30	65	41	7	4	150

Number of Leaves
Average $(M) = 19.2 \pm .053$
Stan. Dev. $(\sigma) = 0.96 \pm .037$

Height of Plants
Average $(M) = 55. \pm .212$
Stan. Dev. $(\sigma) = 3.85 \pm .150$

Coefficient of Correlation $(r) = +.368 \pm .048$

TABLE 2

CORRELATION BETWEEN NUMBER OF LEAVES AND HEIGHT OF PLANT OF #403 "SUMATRA" TOBACCO

Height of Plants in Inches \ Number of Leaves	24	25	26	27	28	29	30	31	
62	1								1
65	1	1							2
68		1	2	4	4				11
71			6	2	6	2			16
74		1	6	7	17	1	3		34
77				6	11	11	8	1	37
80				3	5	8	11	5	32
83				1	2	6	6	2	16
86					1				1
	2	3	13	23	46	28	27	8	150

Number of Leaves
$M = 28.3 \pm .082$
$\sigma = 1.49 \pm .058$

Height of Plants
$M = 76.1 \pm .251$
$\sigma = 4.55 \pm .177$

$r = +.631 \pm .033$

TABLE 3

CORRELATION BETWEEN NUMBER OF LEAVES AND HEIGHT OF PLANT OF (#403X401) "SUMATRA" X "BROADLEAF" TOBACCO

Height of Plants in Inches \ Number of Leaves	19	20	21	22	23	24	25	26	
50	1								1
53									0
56									0
59				1					1
62					1	2	1		4
65	1			7	2	4	2	1	17
68			1	5	12	8	3	1	80
71			2	5	18	18	5	2	45
74				3	8	6	11	2	30
77					6	5	5	2	18
80							1	2	3
83							1		1
	2	0	3	21	47	38	29	10	150

Number of Leaves
$M = 23.6 \pm .072$
$\sigma = 1.30 \pm .051$

Height of Plants
$M = 70.8 \pm .250$
$\sigma = 4.54 \pm .177$

$r = +.406 \pm .046$

leaves all deviations entered to the left of the vertical mean line are negative and all to the right positive, while all deviations of height in inches above the mean horizontal line are negative and those below are positive. Thus, the upper left quadrant contains negative deviations from both series of data — —; the upper right is represented by the signs + for one series and — for the other; the lower left by — and + respectively; and the lower right by + and +. When the *products* of the deviations in each quadrant are computed, (since products of unlike signs are negative and of like signs positive) the upper left and the lower right turn out to be positive quadrants, while the upper right and lower left are negative. Consequently the *degree* and *kind of correlation* are indicated by the distribution of the data in the table with reference to the two mean lines. In the absence of any correlation the data would spread equally in all four quadrants; in positive correlation the upper left and the lower right areas would be most populous; in negative correlation the reverse

would be true. The *degree* of positive or negative correlation is termed the *coefficient of correlation*. This coefficient, *r*, may range from +1 to —1. Perfect positive correlation, in which the two contrasted measurements vary together and equivalently in the same direction, is expressed by +1, while the other extreme, of —1, indicates that the two contrasted measurements vary in opposite directions, that is, as one goes up the other goes down to an equivalent degree. If *r* equals zero, then there is no correlation or causal relationship between the variable characters in question.

One formula for computing the coefficient of correlation is

$$r = \frac{\Sigma D_x D_y}{n\sigma_x\sigma_y}$$

in which D_x and D_y are the deviations of each observed group from their respective means; Σ is the sum of the products; n is the total number of cases observed and σ_x and σ_y are the standard deviations for the two series of observations respectively.[1]

The formula for correlation may be worked as follows:

1. Find the means and standard deviations for each of the two series of data.
2. Determine the deviation from the two means for each item in the table.
3. Obtain the product of these two deviations (regarding signs) and in each instance multiply it by the number of individuals in the group.

[1] The *probable error* (P.E.) of the coefficient of correlation is obtained by the formula

$$\text{P.E.}_r = \pm \frac{0.6745\,(1 - r^2)}{\sqrt{n}}.$$

4. Add the products thus obtained (regarding signs) and divide the sum by the two standard deviations, times the total number of individuals involved.

It will be seen from the coefficients of variation computed for the illustrative tables given, that in "Broadleaf" tobacco plants there is less correlation between the number of leaves and the height of the plant than in the case of an equal number of "Sumatra" plants. The coefficients are $+.368 \pm .048$ and $+.631 \pm .033$ respectively.

Incidentally the third table and its coefficient of correlation, $+406 \pm .046$, reveals the fact that hybrid offspring of "Broadleaf" and "Sumatra" parents are intermediate between the two parental strains in the degree of correlation of number of leaves and height of the plants in inches.

9. The Causes of Variation

With respect to the causes of variation authoritative biologists have taken different points of view.

a. Darwin considered variations as axiomatic. An axiom is self-evident, requiring no explanation. The absence of variations in organisms rather than the occurrence of variations is, from this point of view, the phenomenon requiring an explanation.

Although Darwin clearly recognized the universal occurrence of variations and spent much time in collecting data about them, he was not primarily so much concerned with the causes of variations themselves as he was in utilizing them as a point of departure in establishing an explanation for the origin of species.

b. Lamarck and his followers have regarded the causes of variation either as extrinsic, that is, referable to external factors making up the environment of the organism, such as

food, light, temperature, and moisture, or as intrinsic or physiological, that is, based upon the efforts which an organism puts forth to fit into its particular environment successfully. The causes of variation are to be sought according to the Lamarckian school, in the "environment" and "response" sides of the triangle of life rather than in the "heritage" side (Fig. 1).

For example, Woltereck, by controlling the single extrinsic factor of food supply, was able to modify the height of the

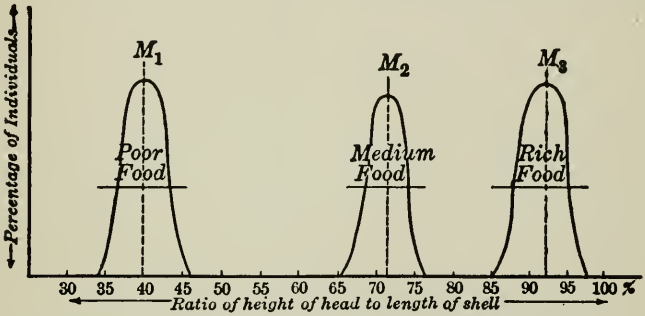
Percentage of Individuals
M_1
M_2
M_3
Poor Food
Medium Food
Rich Food
30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 %
Ratio of height of head to length of shell

FIG. 9.—Schematic curve of the head-height of *Hyalodaphnia* under various conditions of nourishment. Adapted from Woltereck.

"head" of the microscopic fresh-water crustacean, *Hyalodaphnia,* in the remarkable manner indicated in Figure 9. When poor food was supplied, the percentage of the head-height to that of the body averaged hardly forty, while with rich food it was increased to over ninety.

Similarly Klebs succeeded in changing at will the number of stamens in the common "live-for-ever," *Sedum spectabile,* by manipulating the environment in which the plants were kept. Some of his results are shown in Figure 10. Curve *A* combines the data for 4260 flowers which were raised in well-fertilized dry soil under bright light; curve *B* represents 4000

flowers grown in a moist greenhouse under red light; and curve *C* includes 4390 flowers from well-fertilized soil in moist hotbed conditions under a weak light.

Finches fed exclusively on hemp seed, and canaries with red pepper added to their diet take on a deeper hue than ordinarily, while banana flies (*Drosophila*) reared in a constant high humidity exhibit pronounced abnormalities in form

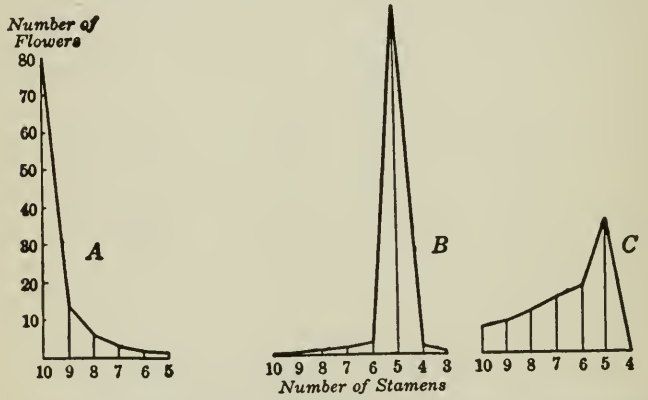

FIG. 10.—Variations in the number of stamens in the flowers of the "live-for-ever" (*Sedum spectabile*) under various controlled conditions. For detailed description, see text. After Klebs.

(Morgan). It is not shown, however, that any of these environmentally induced variations are hereditary.

c. Weismann, on the contrary, believed that the causes of variation, at least of heritable variations in which he was primarily interested, are intrinsic or inborn in the germplasm. His conception of sexual reproduction is that it is a device for doubling the possible variations in the offspring by the mingling of two strains of germplasm (*amphimixis*), which strains may have originated from each other remotely in space and independently in time. By far the greater num-

ber of observations which have been recorded go to substantiate this theory.

Tower found among potato-bettles, for example, that two strains reared in the same environment showed striking differences in variation, a fact necessarily due to intrinsic or hereditary rather than to extrinsic factors. Similar cases may be recalled by anyone.

Nevertheless, heritable variation occurs in the absence of amphimixis so that, at best, sexual reproduction furnishes only one of the possible avenues for the introduction of hereditary variations.

d. Lastly, *Bateson,* whose encyclopedic work "On Materials for the Study of Variation" is a classic, takes the agnostic attitude, that it is rather futile to guess at the causes of variation before the facts are well in hand. He consequently discourages such attempts by saying: "Inquiry into the causes of variation is, in my judgment, premature."

In conclusion, the words of Darwin written over half a century ago: "Our ignorance of the laws of variation is profound," may still be appropriately quoted, notwithstanding the fact that in biometry we have at least an excellent analytical method by means of which considerable insight into variation is being gained.

CHAPTER III

HERITABLE DIFFERENCES

1. The Mutation Idea

Variety is not only the "spice of life" but it is also the central necessity in the origin of new kinds of animals and plants. If there were no variation from generation to generation, then nothing new would appear which nature could in any way seize upon in order to escape from conservative monotony, and as a result there would be no possible evolution in any direction. This deplorable state of affairs we know is contrary to fact.

There are at least three ways, according to Baur, by which an organism can become different from its relatives, viz.—1, modification; 2, combination; 3, mutation. Which of these three ways has been followed in any specific instance can be determined with certainty only by the test of subsequent breeding, for there is nothing in the appearance of an animal or plant to indicate by which of these three paths it has gained any distinctive variation.

By *modifications* we understand those widespread differences which are the result of nurture rather than nature. They are simply environmental effects upon the somatoplasm and consequently are, in all probability, transitory so far as their inheritance is concerned. They are the result of soil rather than seed.

"Combinations" and "mutations" are more deep-seated.

They are conditioned by the germinal nature of the organism and may, therefore, be passed on as hereditary.

Combinations are the result of a new deal after a reshuffling of the cards. Nothing essentially new, which was not already present in one or the other of the parental lines, is introduced but a different arrangement or bringing together of old qualities is effected. This process of variation through hybridization is the concern of Mendelism and will be considered further on.

Mutations, like Minerva springing full-fledged from the head of Jove, are something *qualitatively* new which appear abruptly without transitional steps and that breed true from the very first.

A distinctive qualitative character marks mutations, like the discontinuous differences between such chemical compounds as carbon monoxide (CO) and carbon dioxide (CO_2), as Bateson has pointed out, but the leap from one to the other may be so small that it is difficult to ascertain by inspection whether the difference is due to mutation or to modification. *The test comes in breeding,* since the progeny of a modification, or "fluctuation" as deVries terms it, will revert to the old average of the parental generation while the progeny of mutation will vary around a new average, set by the mutation itself.

The series of positions taken by the lower end of a swinging pendulum illustrates what is meant by these non-heritable fluctuating modifications. They all hold predictable relations to the average position shown when the pendulum comes to rest, because whenever the pendulum is put in motion the various positions all recur as before. A mutation, on the contrary, is represented by a change in the point of attachment at the upper end of the pendulum. It occurs only when the

entire pendulum is unhooked and hung up in a different place. This new point of attachment must be chosen arbitrarily and has no such definite relation to the original attachment as characterizes the variation in position of the swinging end of the pendulum.

When the attempt is made to arrange a series of successive mutations in a curve, they do not ordinarily show a graded relationship to each other as fluctuations do. The latter mass around the average standard according to the laws of chance in much the same way that a hundred shots by a good marksman may center around a bull's-eye. Mutations never group in this way. They find no correspondence even with wild shots at the bull's-eye. They are shots directed at a different target altogether. To use the musician's phraseology, a variation elaborated upon an old theme would correspond to a *modification,* but a *mutation* would be an entirely new theme.

Darwin was fully aware of the existence of mutations or "sports" as he called them, and incidentally gave time to their consideration, but the great task which he set out to accomplish in such a masterly manner was to overthrow the widespread and deep-seated belief of his day in a sudden special creation of distinct species. To this end he marshaled evidence in support of the gradual transition of one species into another, emphasizing fluctuating modifications rather than mutations which seemed to him to play a minor rôle in the origin of species.

Bateson pointed out in 1894 that discontinuous variations, whereby offspring differ decidedly from parents, were much more general than commonly supposed.

It remained for the Dutch botanist Hugo deVries (b. 1849) to be the first to analyze the character of mutations and to focus attention upon them. There is something distinctly

suggestive of Darwin's thorough and cautious method in the fact that deVries worked in silence for twenty years before he gave the world the "Mutationstheorie" with which his name will be forever connected.

2. A Summary of the Mutation Theory

While the mutation theory at the hands of deVries has had to do chiefly with the question of species, in later analysis it has come to be extended more and more to determining genes, which are the units of heredity, rather than to be applied to the organism as a whole.

The main features of the theory with respect to the origin of species may be indicated as follows:—

a. New species arise abruptly, regardless of environment, without transitional forms and at present they are not known to arise in any other way.

b. New forms arise as unusual deviations from the parent form which itself remains unchanged although it may repeatedly give rise to similar deviations.

c. New mutations are, from the first, constant, that is, they produce their like. They do not become gradually evolved as the result of natural selection although natural selection may act upon them after they appear.

d. Among mutations there may occur forms characterized by the addition of something new,—*progressive elementary species,*—as well as forms lacking something present in the parental type,—*regressive varieties.* The latter are the more common.

e. The same mutation may arise simultaneously in many individuals instead of as a single "sport."

f. Mutations do not vary around an arithmetical mean with respect to the parent form, as is the case with fluctuating varia-

tions, but each fluctuates around a new average of its own, thus forming a discontinuous series with the parent form.

g. Mutations may occur in all directions, that is, they are not necessarily definite or orthogenetic.

h. Mutations probably appear periodically.

i. Every mutation means two possible species where one existed before.

j. Useless or insignificant fluctuating variations are not necessarily the material from which natural selection must sift out new species.

k. Natural selection is not a causative agent in evolutionary advance but is simply a sieve which picks out successful survivors from mutations.

l. Mutations do not arise as if by magic in response to the needs of the organism. They may even be harmful, for example, like chlorophyl deficiency in plants, and so be weeded out in nature.

3. Lamarck's Evening Primrose

Perhaps the most widely known plant mutations have been found among the progeny of Lamarck's evening primrose, *Œnothera lamarckiana*. It was these plants that led deVries to formulate his mutation theory.

It is believed by botanists in general that this species is a native of the southern United States, although, so far as is known, it is now extinct as a wild species in America, and native specimens are included in but few American herbaria.

It was exported to London as a garden plant about 1860, and thence it spread to the Continent, where, escaping from gardens, it became wild in at least one locality near Hilversum, a few miles from Amsterdam. Here in an abandoned potato field, it fell under the seeing eye of Hugo deVries in

1885, with the consequence that now both botanist and primrose are famous.

DeVries found among these escaped plants not only *Œ. lamarckiana,* but also two other kinds of mutants, *Œ. brevistylis,* characterized by short-styled flowers, and *Œ. lævifolia,* which has smooth leaves. These two were entirely new species hitherto unknown at the great botanical clearing-houses of Paris, Leyden, and the Kew Gardens.

Since the seeds of the *Œnothera* are produced by self-fertilized flowers, deVries felt safe in regarding these plants as mutants rather than hybrids, and he continued to study them with especial care. Transplanting the mutants along with representatives of *Œ. lamarckiana* to his private gardens in Amsterdam, where it was possible to maintain them in normal healthy condition, deVries was able to follow their individual histories with certainty.

The wild mutants *lævifolia* and *brevistylis* did not reappear under cultivation but he found that, out of 54,343 plants of the species *Œ. lamarckiana* grown as descendants from nine original plants during eight years, there appeared 837 mutants comprising seven different elementary species, all of which, with the exception of *Œ. scintillans,* bred true. See table on the next page.

Some explanatory comment on this table may be of value.

The seeds in each generation were self-fertilized *lamarckiana.*

The mutant *gigas* occurred once, in 1895. From the seeds of this one plant were produced 450 true *gigas* offspring in the first year, and the strain continues to breed true.

Albida was first noted in 1895, but deVries remembered having seen it before and dismissing it as pathological. Because of its poverty in chlorophyll it is a mutant which prob-

MUTANTS OF ŒNOTHERA LAMARCKIANA

GENERATION		GIGAS	ALBIDA	OBLONGA	RUBRINERVIS	LAMARCKIANA	NANELLA	LATA	SCINTILLANS	TOTAL
I	1886–7	..	..	..	..	9	..	..	..	.....
II	1888–9	..	..	..	..	15,000	5	5	..	.....
III	1890–1	..	..	..	1	10,000	3	3	..	.....
IV	1895	1	15	176	8	14,000	60	73	1	.....
V	1896	..	25	135	20	8,000	49	142	6	.....
VI	1897	..	11	29	3	1,800	9	5	1	.....
VII	1898	..	..	9	..	3,000	11	..	..	.....
VIII	1899	..	5	1	..	1,700	21	1	..	.....
		1	56	350	32	53,509	158	229	8	54,343

ably would not maintain itself successfully in nature, although it breeds constant under cultivation.

Oblonga always bred true with the exception of throwing an *albida* in 1895 and a single example of *rubrinervis* in 1899.

Of *rubrinervis* over 2000 invariably bred true, while *nanella* bred true in over 20,000 offspring with but three exceptions, when *oblonga* characters appeared.

Lata, since it produces only female flowers and so cannot be self-fertilized, had constantly to be crossed back with the parent *lamarckiana,* when it produced from 15 to 20 per cent *lata* and 80 to 85 per cent *lamarckiana.*

Finally *scintillans,* which appeared at three separate times, proved constant only in its inconstancy because it invariably produces a heterogeneous progeny. The 1895 plant gave 53 per cent *lamarckiana,* 35 per cent *scintillans,* 10 per cent *oblonga,* and 1 per cent *lata.* One of the 1896 plants gave 51 per cent *lamarckiana,* 39 per cent *scintillans,* 8 per cent *oblonga,* 1 per cent *lata,* and 1 per cent *nanella,* while another 1896 plant gave only 8 per cent *lamarckiana,* but 69 per cent

scintillans, 21 per cent *oblonga,* and 2 per cent of *nanella* and *lata* together.

These different kinds of evening primroses are distinguished from one another by features, involving all parts of the plant, which are unmistakable even to the uninitiated. The old-time systematist would undoubtedly have regarded them as distinct species.

DeVries distinguishes four categories among the *Œnothera* mutants, the first three of which are quite likely to maintain themselves in nature. They are:—

a. Progressive species (*gigas, rubrinervis*), due to the addition of certain characteristics;

b. Retrogressive varieties (*nanella, læviflora, brevistylis*), characterized by the loss of something that was present in the parent form;

c. Inconstant species (*scintillans, lata* and *lamarckiana* itself), that do not always breed true but produce mutants, and

d. Degressive species (*albida, oblonga*), which are defective in some way and are incapable of maintaining themselves in nature.

DeVries' experiments and observations have been repeated on a large scale and extended, notably by MacDougal in the New York Botanical Gardens, by Shull at the Carnegie Institution for Experimental Evolution, Cold Spring Harbor, Long Island, and by Gates in England, and his conclusions have been confirmed in all essential points. The mutability of *Œ. lamarckiana* is as unmistakable and as diverse in America and England as it is in Holland.

The critics of deVries, however, regard *Œnothera la-*

marckiana as a hybrid to begin with, from which different strains have simply been bred out.[1]

Both Bateson and Lotsy have called attention to the presence of deformed or defective germ cells in *Œnothera lamarckiana* as evidence of its hybridity, and Bradley Davis, by crossing *Œ. franciscana* and *Œ. biennis,* has produced a hybrid *Œnothera,* which he has christened *Œnothera neo-lamarckiana* because it not only resembles *Œ. lamarckiana* but behaves like it in producing mutations. He consequently proposes "dissolution of hybrids" as a substitution for mutation in explaining the phenomena that deVries has described.

It is somewhat questionable whether this classical plant, which has added at least a five-foot shelf to the biological literature of the last few decades, is after all the most fortunate organism for demonstrating mutation since its "mutations" may represent simply recombinations becoming isolated from something already present as the result of past hybridization. In either case the new form could breed true and present the behavior of a true mutation. Whatever its value may be in the skillful hands of deVries and his followers in illuminating the problem of mutation, as a form on which to base studies of hybridization, *Œnothera* leaves much to be desired because so many of its seeds are abortive or non-viable that the ratios obtained in the progeny fail to tell the whole truth which is sought.

4. Plant Mutations Found in Nature

The oldest known authenticated case of a plant mutation is the often cited instance of the fringed celandine, *Cheli-*

[1] Any organism, as is well known, can be kept constant indefinitely although in a hybrid condition by means of *balanced lethals* (page 158), which destroy the combinations of like characteristics and permit only the unlike or hybrids to survive.

donium laciniatum, which made its appearance in the garden of the Heidelberg apothecary Sprenger in 1590 among plants of the greater celandine, *Chelidonium majus.* The fringed celandine bred true at once and is now a widespread and well-known species.

The purple beech has appeared historically as a mutant among ordinary beeches upon at least three occasions in widely separated localities, and it has always given rise to a constant progeny.

The Shirley poppy, notable for its remarkable range of color, which was discovered in 1882 by Rev. W. Wilks, originated from a single plant of the small red poppy, *Papaver rhœas,* that is commonly found in English cornfields.

The first double petunia was found in 1855 in a private garden in Lyons (Ziegler). Other instances are known of double flowers among roses, azaleas, stocks, carnations, primroses, etc., arising from single flowering plants, the seeds of which in turn produce double flowers.

The giant primrose is a mutation from a normal strain of known pedigree (Keeble).

"Mutations in certain pericarp color patterns of maize are so common that a wide range of variability results. Selection is able from such material to isolate types relatively stable but very diverse in appearance" (Emerson and Hayes).

That plant mutations may occur in nature and persist successfully without isolation or external selection is shown, for instance, by Schaffner [1] who reports an unusual white verbena growing wild in Ohio over about a square mile of territory along with the typical purplish blue *Verbena stricta* without transitional forms.

Hayes discovered a tobacco mutant in which the average

[1] Ohio Naturalist, Dec., 1906.

number of leaves produced was 70 instead of 20, and Cockerell found a single red mutant plant of the sunflower, *Helianthus lenticularis coronatus,* which has bred true. A few other plant mutations, selected almost at random, are peloric violets; endosperm defect in maize; pitcher-leaved ash; unifoliate adzuki bean; dwarf portulaca; wiry tomato; striped sugarcane; and blotch leaf in maize. The list of similar plant mutations could be almost indefinitely extended.

5. Some Mutations among Animals

In 1791 a Massachusetts farmer, by name Seth Wright, found in his flock of sheep a male lamb with long, sagging back and short, bent legs resembling somewhat a German dachshund. With unusual foresight he carefully brought up this strange lamb because it was an animal that could not jump fences. It occurred to this hard-headed Yankee that it would be much easier to get together a flock of short, bow-legged sheep, unable to negotiate anything but a low hurdle, than to labor hard at building high fences. So it came about that this mutant lamb, in the hands of a man who appreciated labor-saving devices, became the ancestor of the Ancon breed of sheep. Later on this breed gave place in public favor to the merino, also probably a mutant, which produces a superior grade of wool.

Some mutations, like albinism, that may be selected and maintained by man are unlikely to succeed in nature when left to themselves. Albino animals are so handicapped by defective eyesight that they have a hard struggle in the wild condition. Albino rats set free by Dr. Hatai a few years ago upon Goose Island, a small uninhabited bit of land in Long Island Sound, all succumbed in competition with the native rats in a short time. Albinism is a mutation which has ap-

peared not only in man and many domestic animals, such as rabbits, rats, mice, guinea pigs, and water buffalo, but also in foxes, skunks, coyotes, squirrels, birds, and insects.

Hornless cattle suffer fewer injuries from one another than horned cattle. It has consequently become quite a general practice among farmers to "dehorn" their stock surgically. It is an obvious advantage to have cattle born with the hornless characteristic, and many breeds having this feature are now established. In 1889 a mutant among horned stock appeared at Atchison, Kansas, in the form of a hornless Hereford. From this mutant has descended the well-established race of polled Hereford cattle, constituting a bovine aristocracy with registry books and blue blood all their own.

Taillessness in cats, dogs and poultry, as well as hairlessness in rabbits, cattle, dogs, mice, rats, and horses, are further instances of mutations.

Davenport,[1] writing of his experiments with poultry, says: "During the past four years I have handled and described over 10,000 poultry of known ancestry. Of striking new characters I have observed many, some incompatible with normal existence; others in no way unfitting the individual for continued life. In the egg unhatched I have obtained Siamese twins, pug jaws, and chicks with thigh bones absent. There have been reared chicks with toes grown together by a web, without toenails or with two toenails to a toe; with five, six, seven, or three toes; with one wing or both lacking; with two pairs of spurs; without oil-gland or tail; with neck devoid of feathers; with cerebral hernia and a great crest; with feather shaft recurved, with barbs twisted and dichotomously branched or lacking altogether. Of comb alone I have a score

[1] Davenport, C. B., 1909. "Inheritance of Characteristics in Domestic Fowl." Carnegie Institution of Washington, Publication No. 121.

of forms. All of these characters have been offered to me without the least effort or conscious selection on my part, and each appeared in the first generation as well-developed peculiarities, and in so far as their inheritance was witnessed, each refused to blend when mated with a dissimilar form."

Additional animal mutants may be cited as follows:—multi-nippled sheep, double-eared cattle, white canaries, silky fowls, spotted negroes, wattled goats, pink-eyed pigmented guinea pigs, waltzing rabbits, creeping fowls, pacing horses, polydactylous cats, salmon-eyed guinea pigs, and mule-footed swine.

No stock when bred on a large scale breeds absolutely true for all specific characteristics. Gerould reports that in his butterflies (*Colias*), he found blue-green instead of yellow-green eyes, uncoiled instead of coiled tongue, the absence of orthodox wing spots, one proleg less in the caterpillar, etc.

Bateson (1894), in his "Materials for the Study of Variations," gives a detailed list of 886 cases of "discontinuous variations" among animals, many of which doubtless belong to the category of mutations, although several may be "combinations" or must be placed even in the non-inheritable class of "freaks."

The chief reason why definite examples of mutation have been so infrequently noted and recorded is because the attention of the investigator has generally been directed, not to them, but to gradual fluctuating variations which, according to Darwin's conception, furnish the material for the operation of natural selection. Mutations are doubtless much more common than has been generally supposed, and it is likely that they will receive more attention in the future than they have in the past. The banana fly, *Drosophila,* is a famous example of many deviations from type which have been revealed upon

persistent and careful scrutiny. More than four hundred different mutations have been reported for this species alone.

6. Kinds of Mutation

Multiple or *aggregate mutations* are those germinal upsets that affect many parts of an organism instead of a single part. This type, which is a mutation in the deVriesian sense, is in contrast to a *single gene mutation* involving only an hereditary unit that determines a single somatic feature. For example, Babcock describes a new walnut, *Juglans quercina,* which appeared independently in four different widely separated localities in California. This, like deVries' evening primrose, was an aggregate mutation, for differences appeared in size, shape, color and texture of leaves; size, form and color of flower-parts; color of bark, habit of growth, etc. That this was a true mutant and not a hybrid between the oak and the walnut was indicated by negative results in cross-pollinating experiments. Similar aggregate mutations have been reported for cotton, tomato, tobacco, jimson weed, and several other organisms.

Single gene mutations, on the other hand, which may be too slight to differentiate the organism into what may be termed a distinct species, are receiving more and more attention in the analysis of genetic behavior.

Another phenomenon that probably indicates common ancestral germplasm among species at present apparently independent of each other, is the occurrence of *parallel mutations.* The North African ostrich (*Struthio camelus*) and the South Australian ostrich (*S. australis*), although widely separated from each other in space and for long geological time, show, according to Duerden, similar mutations in size, length of neck and legs, skin color and bald head as well as in size and

shape of the egg and the character of its surface, whether pitted or ivory-smooth.

A long list of parallel mutations in *Drosophila melanogaster* and *D. virilis* has been described by Metz, and Sturtevant reports mutations in *D. funebris* that are likewise parallel to those of *D. melanogaster,* in which the occurrence of mutations has probably been more carefully studied than in any other animal.

Sumner with the deer-mouse, *Peromyscus,* has found albinism, spotting, and red-eyed yellow, all mutations known to occur in other mice.

Such mutations suggest that the repertory of mutational change is apparently limited to certain orthogenetic directions and is not indiscriminate or random in its possibilities.

The frequency of *recurrent mutations,* that is, the reappearance of the same mutations, suggests that the cause underlying these irregular hereditary changes is something continuous and definite even if we are at present unable always to put our finger upon it. *Œnothera* has repeatedly shown the same mutations in widely different localities and under the eyes of different investigators. Morgan says of his famous banana flies, "One of the first mutants that appeared, viz., white eyes, has appeared anew in our cultures about three times, in cultures known to be free from it before and not contaminated. The same mutant has been found by several other observers. The eye color vermilion has appeared at least six times; the wing character called rudimentary, five times; cut wing has been found four times, etc."

Reverse mutations have also been repeatedly observed. This is something resembling the unscrambling of an egg. Morgan and Bridges obtained, for example, normal red-eyed flies from white-eyed mutants and May, also with ubiquitous *Dro-*

sophila, got back normal-eyed individuals from bar-eyed mutants.

These facts are arresting when it is remembered that both white-eye and bar-eye, like the great majority of known mutations, are retrogressive in character and are considered to represent the loss of something, for it is surely easier to explain how any hereditary determiner being once present can drop out, than it is to account for its reappearance after it has been lost.

7. The Origin of Mutations

There seems to be no reason why mutation may not occur at any stage in the life-cycle of an organism. In origin a mutation may be *gametic, zygotic,* or *somatic.*

1. A mutation is *gametic* in origin if the onset is in the germ-cell before or during meiosis or the maturation changes which prepare it for union with another germ-cell. In this instance its effect upon the entire development of the individual may be profound and patent, although if it chances to be relegated to an abortive polar cell during maturation (see Chap. X), or to an unmated spermatozoön it will be entirely lost at once. There are no doubt many such "mute inglorious mutations" (Muller) that never see the light of day.

It is furthermore obvious that a gametic mutation usually enters the organism concerned *singly,* that is, from one parent only, and if recessive in character to the corresponding feature in the other parent will fail to put in an appearance in the somatoplasm until some subsequent generation when two hybrids from the new stock each chance to contribute the recessive mutant character in question to the formation of a new individual.

The appearance of such mutants, therefore, unless dominant, must come two or more generations after the mutation has taken place. The time when a gametic mutation is initiated, consequently, and when it manifests itself are by no means necessarily the same. This fact needs to be kept in mind in considering the evidences from experiments on the determining causes or origins of mutations. In the case of sex-linked genes, however, any mutation that takes place in *one* of the x-chromosomes of the mother (Chap. XIII, page 259) is revealed at once if the egg containing it gives rise to a son, because that has but one x-chromosome which always comes from the mother and never from the father. This makes any animal with sex-linked genes excellent material for the study of mutation origins.

Perhaps the reason why mutations are more frequently reported in self-fertilizing (autogamous) plants than in cross-fertilizing (heterogamous) animals is because in self-fertilizing organisms the inbreeding necessary to bring about the doubling of a single character so that it will come into expression is more likely to occur. Moreover, in heterogamous organisms the new forms that appear are more apt to be recombinations than true mutations.

2. A *zygotic mutation* is one which appears in an egg after it is fertilized. In this case the change is evident at once in the resulting individual since the developing individual is the *unfolding* of what is present in the zygote. Such a mutation, for example, occurring *after fertilization* and not as the result of a combination or cross, is reported in tobacco by Hayes and Beinhart.[1]

3. A *somatic mutation,* in contrast to the two kinds of mutations just described which are distinctly germinal in

[1] Science, XXXIX, No. 992, p. 34.

origin, falls directly upon some individual somatic cell or tissue arising out of the original germplasm. Somatic mutations are especially common in plants and may in turn produce such abnormalities as bud variations, chimæras and the like, all of which can be propagated asexually. In such cases all the cells and tissues arising from the mutant somatic cell will express the mutation and no others.

It was a bud variation, for example, which gave rise to the smooth-skinned nectarine from the downy-skinned peach, and similar spontaneous somatic origins of something new that breeds true have been repeatedly observed, particularly among the citrus fruits and various ornamental plants such as roses, dahlias and chrysanthemums.

A *chimæra* is the result of two germinally diverse tissues growing together in intimate contact, each retaining its own original character unmodified by the other. For example, when a scion or twig from a pear tree is grafted upon the limb of an apple tree there may grow out at the scar region of junction between the two different tissues adventitious buds which are made up of cells from both sources. As such a bud grows into a branch the progeny of these two diverse kinds of cells each exhibit the peculiarities of its own kind and a chimæra results with a part of the same branch producing apples and another part pears.

Somatic mutations are particularly characteristic of plants which reproduce asexually, although something suspiciously like somatic mutation appears in the proliferating cells of cancerous animal tissues arising without apparent germinal intervention. In cases of *heteromorphosis* also, or the replacement of one organ or part by another of a different kind following mutilation, as when an excised eye-stalk of a lobster is replaced by an antenna, there is the origination of something

somatically different from what was formerly present, in the absence of sexual reproduction.

Lehmann (1920) proposes the term *metaclonosis* for hereditary somatic modifications, reserving the term *mutation* for solely those instances that involve a change in the genes.

8. When Organisms Mutate

It has been suggested that species may go through the same kind of a life-cycle that individuals do, only taking infinitely more time to do it. As shown in Figure 11, they are born of other species and enter the prodigious growth period of infancy and youth, both of which are characterized by much fluctuation. With maturity they gradually become comparatively stable until the reproductive period is reached, when they throw off their progeny, as on a tangent. They finally pass into the excessively differentiated period of old age, from which there is no recall, although they approach in many features the infantile condition, and end in death or extinction. This cycle is repeatedly illustrated by phylogenetic lines of fossil forms which have long since become extinct.

Beecher has pointed out that in paleontological times, just before they became extinct, species often underwent extreme specialization either in the form of fantastic shapes, an excessive number of spines or elaborate sculpturings as seen on the shells of ammonites, belemnites, and trilobites, or of gigantic size as in the dinosaurs, plesiosaurs, and theromorphs. All of these facts indicate a *species-cycle* in which these abnormal features were the unmistakable signs of old age.

The reproductive period of a species when mutants are being thrown off, as of an individual, may extend over a considerable period of the whole cycle, or it may be confined to a relatively small segment. It is possible that in the evening

primrose deVries may have caught a plant passing through the crucial period of species-reproduction.

Another reason why so few mutations have as yet been seen may be because the majority of organisms are not, during the short span of human observation, passing through the reproductive part of their cycles. When it is remembered that accurate observation with the detection of mutations in view has extended over only a brief period, insignificant in comparison with the vast geologic stretches of time concerned in species-building, the marvel is that so much, rather than so little, has been seen.

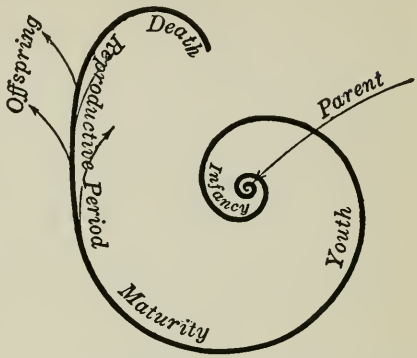

FIG. 11.—Diagram of the relation of reproduction to the life-cycle.

9. Possible Causes of Mutation

The conclusions in this paragraph could be better presented no doubt after the consideration of the remaining chapters of the book, particularly the section on the cellular basis of heredity (Chaps. X, XI and XIII), but some discussion, nevertheless, seems desirable at this point, even if it may be necessary to return and reconsider it later.

There are at least three avenues of approach to the analysis of mutation: (1) *anatomical,* depending upon observation of its occurrence both in nature and under control; (2) *genetical,* consisting of the experimental breeding of test cases, and (3) *cytological,* or the microscopic examination of the germ-

plasm. It is this latter method that furnishes perhaps the most hope of gaining some insight into the fundamental causes underlying the phenomena of mutation.

Babcock and Clausen have classified mutations from the cytological standpoint into two groups, viz., *chromosomal aberrations* and *factor mutations*. Chromosomal aberrations are accidents or irregularities occurring in the nuclear make-up of the germ-cells. These aberrations may be of various kinds and probably take place during meiosis when the germ-cells are going through the preparatory process of reduction of the chromosomes which precedes the formation of the fertilized egg.

For example, in the unpairing of homologous chromosomes after they have come to lie in contact with each other during the process of syndesis, it is conceivable that the process may not be clean-cut and complete but that a piece of one chromosome may adhere to its mate thus changing its size and composition. Or again, a fragment of a chromosome, during the complicated elimination processes accompanying the marriage ceremony of germ-cells, may be shuffled out and lost, thus creating a deficient chromosome. Such accidents to the germ-cells would be reflected in all the subsequent mitotic divisions of the somatic cells derived therefrom and a mutation would be the result. At any rate, an examination of the nuclear structure of mutants frequently reveals chromosomal irregularities so that an unmistakable relation between chromosomes and somatic structures undoubtedly exists.

Another irregularity that sometimes occurs is an unequal migration of the chromosomes to the poles of a germ-cell during the reduction division, which results in a cell progeny of mature gametes having a number of chromosomes unlike the number in the normal gametes. This appears to be the

reason for the mutation, *Œnothera lata,* which has 15 chromosomes instead of 14, the typical number for *Œ. lamarckiana* from which it sprang. What occurs in the formation of this mutation is that for some reason *Œ. lamarckiana* during reduction division instead of dividing as usual into 7-7 makes the unequal division of 6-8, a phenomenon known as *non-disjunction* (Bridges). When this 8-chromosome gamete joins with a normal 7-chromosome gamete the new mutant number of 15, characteristic of *Œ. lata,* is the result.

Gates and others in their extensive cytological studies on *Œnothera* mutants, have found not only 15 chromosomes instead of the normal 14 but also, associated with various other mutations, the abnormal numbers of 20, 21, 22, 23, 27, 28, 29, and 30.

Œnothera gigas is a mutant in which 28 chromosomes, or twice the normal number, appear and, moreover, these chromosomes represent actually twice the original amount of chromatin material. *Gigas* mutants have been found in various other forms, such as the tomato (Winkler), the jimson weed or *Datura* (Blakeslee and Belling), *Primula* (Gregory) and *Narcissus* (Stomps), that are always characterized by a doubling of the chromosomes. This condition is termed *tetraploidy* because it shows four times the gametic number of chromosomes.

Among animals at least two cases of tetraploidy have been reported, namely, a two-chromosome and a four-chromosome type of the worm *Ascaris,* which have been long known, and a forty-two-chromosome and an eighty-four-chromosome type of the brine shrimp *Artemia salina.*

When a normal diploid *Datura* is crossed with a tetraploid *gigas* individual, a triploid mutant results with a different constellation of somatic characters, so that the best of evidence

is now at hand for one category of mutations at least, that of chromosomal aberrations, which is dependent upon, or associated with, abnormal *quantitative* differences in the chromosomes. Blakeslee and Belling have furthermore demonstrated that, with the formation of tetraploid *Daturas,* "unbalanced types" may occur in which one of the 12 sets of quadruple chromosomes characteristic of this plant may have added to it one or more extra chromosomes, or on the other hand, any single set of the 12 may suffer the loss of one or more of its four tetraploid chromosomes.

In all such instances of "unbalance" or abnormality in the number of chromosomes the plants themselves show corresponding deviations from the normal condition in their visible characteristics.

The other category of mutations, *factor mutations,* is *qualitative* and concerns the nature of hereditary units or genes rather than quantitative groups of these genes as they are assembled in the chromosomes.

The bearing of the whole matter of mutation upon heredity lies in the fact that, contrary to Darwin's belief, it is apparently mutations and recombinations, and not fluctuations or modifications, that make up heritable variations. If this supposition proves to be true, mutations furnish the essential material in the study of heredity. Consequently, whatever knowledge we may gain of them has a direct relation to the entire problem of genetics.

Whatever it is that causes the character of a gene to change in quality, with the resultant expression in the somatoplasm, is still a matter of doubt. Some investigators find satisfaction in assigning external environmental causes to the solution of the problem while others prefer to conceal their ignorance under the blanket of "internal causes," whatever these may

be. At least it is reasonable to say, when a new variety appears suddenly in a bottle full of banana flies or in a field of plants in the same environment with all of its unmodified fellows, that mutation can arise *somehow* without outside interference.

The wild jungle fowl presents a large and useful series of mutations which have cropped out in poultry under the spell of domestication while the goose, on the contrary, although domesticated for an equally long period, has remained practically the same. The *nature* of the plastic hen must be different from that of the more conservative goose.

Among the most conspicuous advances in inducing mutations by outside interference are the experiments initiated by Muller [1] upon *Drosophila* with x-rays. Muller says, "It has been found quite conclusively that treatment of the sperm with relatively heavy doses of x-rays induces the occurrence of true 'gene mutations' in a high proportion of the treated germ-cells. Several hundred mutants have been obtained in this way in a short time and considerably more than a hundred of the mutant genes have been followed through three, four, or more generations. They are (nearly all of them, at any rate) stable in their inheritance, and most of them behave in the manner typical of the Mendelian chromosomal mutant genes found in organisms generally."

In the short time that has elapsed since Muller's pioneer work, many other investigators have utilized this method of approach not only with banana flies and various other animals but also with a wide range of plants, and there is every indication that in radiation a biological Klondike has been opened up.

Not only true *gene mutation,* but also "crossing-over" and "chromosome breakage," to be considered later, have been in-

[1] "Artificial Transmutation of the Gene." Science 66, p. 84. 1927.

duced experimentally by short-wave radiation. Both of these types of chromosome rearrangement result in visible characters that are indistinguishable from true mutations.

In answer to the objection that x-rays and radium are too unusual or artificial sources of genetic modification to have played any considerable part in bringing about mutations in nature, it may be pointed out that modern physics has already demonstrated how we live in an environment made up of various radiations and vibrations, all the way from ultra-violet to "cosmic rays," to an extent utterly unsuspected until a short time ago.

The secret of the causes of mutations still remains a challenge to every skilled geneticist who uses the indispensable tools of observation and experimentation.

CHAPTER IV

THE INHERITANCE OF ACQUIRED CHARACTERS

1. Summary of Preceding Chapters

Hereditary resemblance is due to the derivation of offspring from the same stock as the parent, and successive generations, therefore, are simply periodic expressions of the same continuous stream of germplasm.

Perfect inheritance, or uniformity in the individuals of successive generations, does not exist, since variations always occur. It is upon these variations that evolution depends. Without them there would be no change of type and consequently no possibility of evolutionary advance.

Some variations are fluctuating or intergrading in character and may be detected and analyzed by statistical methods, while others are mutations, or discontinuous variations, representing qualitative differences which do not lend themselves readily to statistical analysis.

Mutations are more common than was formerly believed, and since they are usually germinal rather than somatic in character, they play an important rôle in heredity.

2. The Bearing of this Chapter upon Genetics

Only those variations which reappear in succeeding generations have to do with heredity. Hence it becomes important to inquire as to what kind of variations actually reappear. Can variations that are not inborn, but which are acquired during

the lifetime of the individual, be inherited? Does the experience of the parent become a direct part of the child's heritage, or can the environment or the behavior of the one enter in any way into the heredity of the other? Can changes wrought in the somatoplasm be so impressed upon the germplasm as to change it in such a way that it, in turn, will give rise to similarly modified somatoplasm in the next generation? To use Shakespeare's antithesis,[1] can *nurture* as well as *nature* be transmitted? As Conklin says: "Few questions have been discussed so fully and so fruitlessly as this."

In answering these questions we are of course concerned solely with *biological inheritance* and not at all with those extra-biological accumulations in the way of arts, literature, tradition, invention, and the like which constitute civilization and which make us the "heirs of the ages." Such benefits are entailed upon us much in the same way as property is "inherited," but they form no part of the personal biological heritage into which we are now inquiring.

3. The Importance of the Question

This inquiry concerning the inheritance of acquired characters, which Professor W. K. Brooks has called "the interminable question," is not simply an academic matter. Its solution is of vital importance from several viewpoints. For breeders, who are trying to maintain or improve particular strains of animals or plants; for physicians, who, in fighting disease, are honestly seeking to substitute an ounce of prevention for a pound of cure; for sociologists and philanthropists, who have at heart the permanent bettering of human conditions; for educators, who cherish hopes that their life-

[1] "A devil, a born devil on whose nature
Nurture will never stick."—"Tempest," Act IV, Sc. 1.

work of unfolding the youthful mind may prove cumulative and lasting rather than transitory; for religious workers, who want their faith strengthened that conquests in character-building may outreach the individual and so enrich the race; for parents, who entertain hopes that their own efforts may give their children a better biological start in life,—for all these and many more, it is important to know the answer to the question: Can acquired characters be inherited?

4. An Historical Sketch of Opinion

That the personal accumulations of a lifetime are heritable was generally believed throughout the credulous ages. Over a century ago Lamarck (1744-1829) made this idea the cornerstone of his theory of evolution. It was all very simple. The reason evolution occurs in nature is because individual acquirements are being continually added to the onflowing stream of living forms. This cumulation of characters, indeed, *is* evolution. How else can the present stage of adaptation of organisms to their several niches in nature be explained save by seeing in it the final results of generations of gradually-accumulating inherited adaptations?

Darwin also believed in the inheritance of acquired characters, although he differed from Lamarck with respect to how such characters are acquired.

Francis Galton in 1875 was one of the first to express skepticism regarding this generally accepted belief, but the man who, in a masterly manner focussed the growing doubt, and who did more than any other to inspire thought and investigation upon the subject, was August Weismann, who conspicuously bore the torch of genetics between 1880 and 1890. Weismann made the issue so clear that the heritability of acquired characters became the parting of the ways which

divided biologists into the two camps of *Neo-Lamarckians* who affirm, and *Neo-Darwinians* who deny, such inheritance. His conclusions, which are the natural outgrowth of the theory of the "continuity of the germplasm," were based, however, upon purely logical rather than upon experimental grounds.

Comparative anatomists and paleontologists, who are accustomed to work from results back to their causes, are frequently inclined to look favorably upon the inheritance of acquired characters while, on the other hand, geneticists and embryologists, representing the two lines of study which furnish the most immediate approach to this problem, are well-nigh agreed that acquired characters are not inherited. Experiment from cause to effect is undoubtedly the best criterion, for if the question could be decided by a vote or by an expression of opinion, the result would be doubtful, since each column contains the names of men whose scientific accomplishments entitle them to a respectful hearing. But just what are the facts of the case?

5. Confusion in Definitions

The source of much of the lack of agreement in this controversy lies in the definition of what constitutes an "acquired character." One is reminded of the two knights who fought bitterly over the color of a shield, one maintaining that it was red, the other that it was black. So they hacked away at each other, as all good knights should do in the defense of the truth, until they both fell down dead beside the shield which was black on one side and red on the other.

"Characters represent the end results of a long chain of processes in which environmental influences interact with hereditary dispositions all along the line" (Hogben), but it is

only these "hereditary dispositions," packed away in the chromosomes, that are the material of actual inheritance.

Except in some kinds of asexual reproduction actual characters are never inherited, but only the determiners or potentialities which regulate the way in which the organism reacts to its environment with respect to the characters in question. Reid has pointed out that in one sense every adult character is "acquired" because it has no expression at first. For instance, there is no beard on the face of a male infant, but one will presumably be acquired later on in the life-cycle due, however, to a heritable and not to an environmental cause.

It is plain that every new character which represents a forward evolutionary step must have been "acquired," in the sense of being added, sometime and somewhere, else it would not be present, as there is evidence that it is. Perhaps the question, as Montgomery has suggested, ought to be changed to read: "*What kinds* of acquired characters are inherited?" It is obvious that discussion is futile until a common denominator in the shape of a definition of acquired characters shall be agreed upon.

6. Weismann's Conception of Acquired Characters

Weismann defines an acquired character as *any somatic modification that does not have its origin in the germplasm.*

Those somatic modifications which are the regular phases of the developing individual, such as the acquisition of a deeper voice by the male at puberty or the substitution of the permanent dentition for the milk-teeth, are somatic variations which have their rise and control in the germplasm and consequently cannot properly be included under the head of acquired characters.

Examples of acquired characters in the Weismannian sense are mutilations, the effects of environment, the results of function as in the use or disuse of certain organs, and such diseases as may be due either to invading bacteria or to the neglect or misuse of the bodily mechanism.

7. The Distinction between Germinal and Somatic Characters

Redfield has thrown light on the classification of the characters which make up the individual by quoting the familiar lines:

> "Some are *born* great,
> Some *achieve* greatness,
> Some have greatness *thrust* upon them."

"Born" characters are constitutional, having their origin in the germplasm itself. They are never Weismannian "acquired characters" and may be illustrated by eye-color, mental disposition, or facial features. Lightning calculators and musical prodigies may have their gifts developed and enlarged, but the fact that their talent is nevertheless an unmistakable gift, and not an acquisition, remains true.

"Achieved" characters are functional and are gained by exercise or individual effort. Many things are achieved which are not acquired characters, as, for instance, wealth, reputation, social position, or an education. Not any of these achievements, however, are biological characters, and therefore we are not concerned with them in this connection, although in the case of education it should be noticed that the mental exercise necessary to bring about a trained mind, if not the subject matter of the education itself, is distinctly an acquired character of the "achieved" type.

"Thrust" characters are the results of environment. They are

acquired without functional activity on the part of the organism and usually in spite of anything the organism can do to prevent. Sometimes these characters are even thrust upon the individuals before birth, as in the case of blindness caused by parental gonorrhea, or tuberculosis arising from uterine infection, in which case they are termed *congenital* characters.

Congenital or prenatal characters, however, are in no way the same as germinal characters, for they fall just as truly into the category of acquired variations as do those which make their appearance in later life.

8. What Variations Reappear?

Returning now to Montgomery's question,—"What kinds of acquired characters are inherited?"—it is apparent that only the "born" ones can be, which have their roots in the germplasm whence the new individual arises, and that "achievements" and "thrusts," in order to reappear in the succeeding generation, can do so *only by first becoming incorporated in the germplasm,* from which all "born" characters are unfolded in the course of development.

The determiner for any character or type of reaction that is not acquired must have been present in the germplasm from which the organism arose, as *there is no transfer of characters between organisms except through the germ-cells.* Thus it is evident that the only inherited acquisitions are those which, either primarily or secondarily, bring about variation in the germplasm, from which the somatoplasm arises. Such temporary acquisitions as a coat of tan or a display of freckles, for instance, do not impress the germplasm, for when the cause that incites their appearance is removed, they soon vanish.

9. How May Germplasm Acquire New Capacities

In addition to mutation, which was considered in the last chapter, various sorts of rearrangement in the germplasm may present something different in the somatoplasm.

First there may be mentioned the "amphimixis" of Weismann, that is, the mixture of two nearly related strains of germplasm in sexual reproduction within a species, and second, the mixture of two more remotely related strains resulting in hybridization. In either case the strain of germplasm undergoes a shake-up that may result at least in new combinations of characters, or better expressed, capacities to produce characters, if not in the production of entirely new capacities. This recombination of capacities by means of amphimixis and hybridization will receive further attention in a later chapter.

The fact that successive parthenogenetic generations, in which amphimixis does not of course occur, may show even a larger degree of variability than sexually produced generations, indicates that amphimixis in itself is by no means sufficient to account for all kinds of hereditary variations.

It is conceivable that the external factors that act upon the germplasm may be grouped into three classes: first, external factors acting upon the somatoplasm and then through the agency of the somatoplasm affecting the germplasm ("somatic induction" of Detto, or "pangenesis" of Darwin); second, external factors acting directly upon the germplasm and the somatoplasm at the same time ("parallel induction" of Detto); and third, external factors acting upon the germplasm without necessarily at the same time having any effect upon the somatoplasm.

Many instances of the apparently direct influence of external

factors upon germplasm are known in biological literature, and these have led to some of the misunderstandings concerning the "interminable question" of the inheritance of acquired characters. Sitkowski fed the caterpillars of the moth *Tineola biselliella* with an aniline dye (Sudan red III), obtaining therefrom, instead of normal whitish ones, moths that laid colored eggs, and these in turn hatched into caterpillars still tinged with the color of the red dye. Riddle, with guinea pigs, and Gage, with poultry, obtained quite similar results. These cases of apparent parallel induction, however, are not a matter of inheritance at all, since the germinal substance itself was not involved, but of animals who got their red color directly from external sources while they were eggs within the mother's body.

10. Weismann's Reasons for Doubting the Inheritance of Acquired Characters

Weismann's reasons for questioning the popularly accepted view that acquired characters are inherited may be briefly stated as follows:

First, there is no known mechanism whereby somatic characters may be transferred to germ-cells.

Second, the evidence that such a transfer actually does occur is inconclusive and unsatisfactory.

Third, the theory of the continuity of the germplasm is sufficient to account for the facts of heredity without assuming the inheritance of acquired somatic characters.

Let us examine these three statements a little more closely.

A. No known mechanism for impressing the germplasm with somatic acquisitions

Each germ-cell remains an independent unit and does not participate in the activities of the body but lies within the body

like a commensal or parasite. As Castle expresses it, "Germ-cells are guests of the body, not members of the household." It is hard to see, therefore, how a germ-cell can be changed except in a general nutritive way which is quite different from a change in character of any hereditary significance.

Abnormally small beans, for example, because of the restricted nutriment stored in their undernourished cotyledons, tend to carry over their defective size to the next generation. This stunting is not a case of the inheritance of an acquired characteristic, however, but is due to the fact that the small bean with its deficient food-storage is unable to form a normal seedling. This is a temporary and not a permanent modification.

The somatoplasm is something that has developed from the original fundamental germplasm along the paths of differentiation and elaboration. The more complex the body-cells become, that is, the more successive modifications they undergo, the more difficult it is for these elaborated somatic cells to return to their original primitive germinal estate.

In many lower forms of life where cell elaboration is not so great, a part lost by amputation is often regenerated, but this process is not possible in higher forms where the parts represent cell complexes too hopelessly differentiated to begin anew the unfolding sequences of their elaboration. This difficulty was a very real one in the mind of that famous nocturnal inquirer Nicodemus when he asked: "How can a man be born when he is old? Can he enter a second time into his mother's womb and be born?"

Not only the development of the race which we call evolution, but also the determination of the individual in heredity, is a *chain of onward-moving sequences* like the succession of events in history. It is hard to see how recent events can

influence preceding events. It is hard to see how the water that has gone over the dam can return and affect the flow of the river upstream in any direct way. It is likewise difficult to understand how differentiated somatoplasm, which represents an end stage of a successive series of modifications, can make any definite impress upon the original germplasmal sources from which it arose.

Darwin felt this difficulty and presented with apologies his provisional hypothesis of *pangenesis* to explain the inheritance of acquired characters in heredity and the process of regeneration of lost parts.

Pangenesis assumes that every bodily part sends contributions to the germ-cells in the form of "gemmules." Such gemmules, or hypothetical somatic delegates, then reconstruct in the germ-cells the characters of the entire body, including acquired modifications as well as all others, and thus there is no theoretical reason why acquired characters cannot be transmitted. Unfortunately there is no tangible basis in fact for this delightfully simple explanation to rest upon. It is an hypothesis assuming that *all parental somatic cells* take part in the formation of the new individual, hence it was called "pangenesis," or *origin from all.*

Nothing we have subsequently learned of minute cell structure favors this hypothesis, while many facts go quite against it. Blood transfusion experiments, as demonstrated by Galton, are entirely negative so far as the transfer of characters through hypothetical pangenes or gemmules in the blood from one individual to another is concerned. Moreover, pangenesis is directly opposed to the theory of the continuity of germplasm so convincingly set forth later on by Weismann. Darwin indeed advanced the idea of pangenesis only in the most tentative way, being entirely ready to see it abandoned at any

time for something better. It performed at least one valuable service to science, namely, that of demonstrating how far investigators were from an adequate conception of any means by which somatic modifications might become incorporated in the germ-cells.

We must acknowledge, however, with Lloyd Morgan that the fact that a mechanism for the transfer of somatic characters to the germ-cells has not been discovered, is not proof that such a mechanism does not exist. It may simply be beyond our present powers of penetration.

B. EVIDENCE FOR TRANSMISSION OF ACQUIRED CHARACTERS INCONCLUSIVE

The evidence for the inheritance of acquired characters was, for a long time, taken for granted. This hypothesis was the most obvious explanation of many facts and so was accepted without question. The most obvious interpretation, however, is not always the correct one. The sun, for example, appears to go around the earth, but astronomers assure us that it does not.

When Weismann began to sift the evidence for the inheritance of acquired characters, he found that it was largely based upon opinion rather than fact, much like the popular belief with regard to the causation of warts by handling toads.

The supposed evidence for the inheritance of acquired characters falls chiefly into the following categories:

a. Mutilations;
b. Environmental effects;
c. The effects of use or disuse;
d. The transmission of disease;
e. Immunity;
f. Prenatal influences.

a. Mutilations

It is fortunate that the sons of warriors do not inherit their fathers' honorable scars of battle, else they would now be a race of cripples.

The feet of Chinese women of certain classes have for centuries been mutilated into deformity by bandaging, without the mutilation in any way becoming an inherited character. The same result is also true of tattooing and of circumcision, the latter a mutilation practiced from ancient times by the Jews and certain other Eastern peoples.

The progressive degeneration or crippling of the little toe in man has been explained as the inheritance of the cramping effect of shoes upon generations of shoe wearers, but, as Wiedersheim has pointed out, the fact that Egyptian mummies show the same crippling of the little toe is unfavorable to this hypothesis, for no ancient Egyptian could ever be accused of wearing shoes of the modern foot-crippling type or of having had shoe-wearing ancestors. Sheep and horses with docked tails as well as dogs with trimmed ears never produce young having the parental mutilation.

Weismann's classic experiment with mice, an experiment subsequently confirmed by others, is additional negative evidence upon this same point. What Weismann did was to breed mice whose tails had been cut off short at birth. He continued this decaudalization through twenty-two generations with absolutely no effect upon the tail-length of the new-born mice. One could formerly see in the catacombs of the *Zoologisches Institut* at Freiburg, filed carefully away on shelves, as a "document," long rows of labeled bottles containing the fifteen hundred and ninety-two martyrs to science which made

up the twenty-two generations of mice in this famous experiment.

Blaringhem, it is true, obtained mutations which bred true from latent buds that were forced into development following mutilation of normal buds, but Griffon has shown that similar mutations occur with preceding mutilations, so that this, as Shull points out, is simply a case of segregation of biotypes already present in the mutilated parent.

It must be admitted that mutilations furnish a very poor criterion for the inheritance of acquired characteristics since it is the modification and not the destruction of parts that is the subject of inheritance.

Conklin has hit the nail upon the head with respect to mutilations by saying: "Wooden legs are not inherited, but wooden heads are."

b. Environmental Effects

Trees deformed by prevailing winds, like the willows that line the canals in Belgium and Holland, or storm-crippled trees along the exposed seacoast, are not known to produce a modified progeny when the adverse environmental conditions in which the parental trees lived are removed. Similarly, the persistent sunburn of Englishmen long resident in India does not reappear in their children born in England.

Sumner kept mice in a constant but abnormally high temperature at 26° C. with the result that the ears, tail, and feet grew noticeably larger than in control animals kept in ordinary lower temperatures, while at the same time the general hairiness of the body decreased. These modifications reappeared in varying degree in the offspring when subjected to normal temperatures. It should be remembered, however, that mice are mammals that pass through an extended uterine

existence, so that it is easy to see how the offspring in this case were subjected to the same excessive temperature as the parents for a period sufficient to amply account for their subsequent variation when removed to a normal environment.

Zederbaur found that the wayside weed *Capsella,* which in the course of many years has gradually crept along the roadsides up into an Alpine habitat and there "acquired" Alpine characters, upon being transplanted to the lowlands retains its Alpine modifications. Although this case has been cited as an authentic instance of the inheritance of acquired characters, is it not possible that the conquest of the Alps by *Capsella* has been due, in the course of time, not to the inheritance of acquired characters at all, but to a gradual natural selection of just those germinal variations which best fitted it to cope with Alpine conditions until, finally, a strain of germplasm producing somatoplasm suitable to Alpine conditions has been isolated in the form of an elementary species derived from the original type? If this is what has happened, of course such germplasm would naturally give rise to Alpine plants whether individual plants grew to maturity near the snowline or in the warm valleys at a lower altitude.

Kammerer, by reducing the water supply, is said to have succeeded in transforming *Salamandra maculosa,* a salamander normally producing about seventy eggs which, when hatched in water, become gill-breathing tadpoles, into a salamander producing only two to seven young which are born alive without gills and are able to live out of water entirely, in damp situations. These land-adapted offspring, moreover, when supplied with abundant water, produce in turn tadpoles which spend days only, instead of months, in the water undergoing their metamorphosis, thus showing an apparent inheritance of an acquired character.

It should be pointed out, however, that in these cases the gill-breathing forms in each instance represent arrested development. For example, another salamander, the Mexican axolotl, when kept under observation for a prolonged period, turns out to be simply the larval form of *Amblystoma,* which was formerly thought to be a distinct species. Under normal conditions of an abundant water environment and relatively high temperature it gets no further in its metamorphosis than the axolotl or tadpole stage, when it produces eggs and sperm and finishes its life story. A change in environment simply permits the life-cycle to go on further before egg production. Changing from gill-breathing to lung-breathing is not, therefore, an acquired character, but a purely germinal character that may be either blocked or released by changing conditions in the environment. The phenomenon of sexual maturity in the larval stage is termed *neotony.*

c. The Effects of Use or Disuse

The callosities on the end of a violinist's left-hand fingers are acquired by use, but they are not inherited. There are callosities on the knees of the wart-hog, *Phacochærus,* which are also apparently the result of use, for these animals kneel as they root for a living in the African forests, and have done so for untold generations. It has been noticed that young wart-hogs, however, as soon as they are born possess the callosities, so that this instance looks like one of inheritance of a character acquired through use or exercise. Duerden also describes callosities at frictional points in embryonic ostriches which have not as yet had any opportunity to acquire these modifications by use.

The skin on the soles of human feet is thicker than the skin elsewhere, and by use it becomes still thicker. This is appar-

ently another instance of the same sort. The writer has observed, however, that a cross-section through the foot of a "mud puppy," *Necturus maculatus,* shows a much thickened sole. *Necturus,* it should be noted, is a very primitive salamander living always under water and never using the soles of its feet in any way to bear its weight, nor is it reasonable to suppose that it ever had any ancestors who did so, for the hands and feet of the Amphibia are the most primitive and ancient hands and feet to be found in an evolutionary way in the animal kingdom without any known ancestral types. The thickening of the skin on the sole of the mud puppy's feet may be due, therefore, to germinal determiners, in which case it is in no way an acquisition through use. The same may also be true of the wart-hog's knees, Duerden's embryonic ostriches and human soles.

The strong arm of the stevedore, the skilled hand of the artisan, and the trained ear of the musician, are not inherited. They have always to be reacquired in each succeeding generation just as surely as the ability to ride a bicycle, or to read and write.

Herbert Spencer has defined instinct as "inherited habit." But surely those instincts which determine a single isolated action during the lifetime of the individual, such as the spinning of a peculiar cocoon or depositing eggs upon a specific food plant, cannot be the result of habit, since habits are formed only through repeated action.

Dr. Hodge, who succeeded in hatching tame quail chicks out of "wild" eggs, asks the pertinent question: "How can a *fear* hatch out of an egg?" The habit of wildness, particularly with precocial chicks like quails, may, under an inciting environment, be very soon established after hatching, but it is difficult to see how caution, gained by the experience of the

parents, can find its way into the fertilized egg. Does the setting instinct of the hen, for example, arise because her ancestors formed the habit which subsequently becomes inherited, or does some physiological urge inherent in the germplasm cause setting behavior in the hens of each generation, regardless of what her ancestors did?

If, then, *some* instincts require a different explanation from that of "inherited habit," may it not be likely that all instincts do? Is it not better to assume that the structure of the germplasm determines a particular response to a particular stimulus regardless of whether in the past the ancestors have made a similar response to a similar stimulus?

d. Transmission of Disease

If acquired diseases were heritable we would all have been dead long ago. When a son, whose father died of pneumonia, succumbs himself to pneumonia after an interval of years there may be no more causal or hereditary connection between the two events than when a second house burns down on the same site where a former house went up in flames.

Many diseases, like tuberculosis, have their immediate cause in invading pathogenic bacteria. Bacteria themselves cannot be inherited for the reason that it is not possible for them to become an integral part of the fertilized egg and thus cross the "hereditary bridge" which joins two generations. A general predisposition to bacterial disease, that is, a lack of resistance to bacterial invasion due to defectiveness in physical or physiological equipment, may be present as a combination of characters in the germplasm, or an individual, as the result of disease, may "acquire" a generally weakened germplasm and so produce a progeny exhibiting general liability to disease; but it is doubtful if such a condition can properly be

termed the inheritance of an acquired character, since the particular definite disease in question is not demonstrably heritable.

When alcoholism "runs in a family," its reappearance in the son is probably due to the fact that he is derived from the same non-resistant strain of germplasm as his father. The fact that the father succumbed to the alcohol habit is not the determining cause of drunkenness in the son. The same thing that caused the father to become an alcoholic, namely, weak germplasm, and not the resulting drunkenness in the parent, is probably the causal factor for alcoholism in the son.

The susceptibility of individuals having certain types of body-build and temperament to particular diseases is well established. Both Tyzzer and Little, for example, have demonstrated the existence of susceptible and immune strains of mice as far as some types of cancer are concerned. In man it is a matter of general observation that some races, such as American Indians, Australian aborigines, full-blooded Africans, and Polynesians, are mostly immune to cancer. Among Japanese women cancer of the breast is only about one-tenth as common as among European women. These facts suggest a difference in the fundamental germinal make-up of races with regard to disease susceptibility, rather than the inheritance of acquired parental deficiency.

At the same time it is entirely probable that hereditary alcoholism may in some cases arise through "parallel induction," affecting parents and offspring at the same time, that is to say, acquired alcoholism may end in the simultaneous poisoning and consequent modification of both the somatoplasm and germplasm of the parent, with the result that the germplasm has less resistance to alcoholism in a succeeding generation. The offspring are consequently more likely to

succumb to the disease. This, however, is not the inheritance of an acquired character or of a definite somatic modification in the Weismannian sense.

When a man of the present generation has rheumatic gout, it is a severe stretch both of patriotism and of the powers of heredity to trace the origin of the affliction back to a revolutionary ancestor who acquired sciatic rheumatism by sleeping on the ground at Valley Forge, yet this is quite as direct as many alleged instances of the inheritance of disease.

In the majority of instances, apparent cases of the inheritance of disease are merely instances of *reinfection.* This reinfection of the offspring may occur very early in embryonic life, even in the egg, as in the case of pebrine in silkworms (Pasteur), in the tick which transfers the protozoan parasite causing Texas fever, and in the bacillus which causes white diarrhœa in poultry. Or it may happen after birth, provided the offspring are exposed to the same environment as that in which the parent acquired the disease. In any case *reinfection is not inheritance.*

e. Immunity and the Effect of Drugs

Ehrlich subjected mice to increasing doses of ricin until they became immune to doses which are ordinarily fatal. When these ricin-immune mice were bred to non-immune mates the offspring in turn showed some degree of immunity *if the immunized parent was a female* but not if the immunized parent was a male. In other words, the immunity was transferred only through the female, where the blood of the mother is for a considerable period during fetal life in intimate relation with the blood of the offspring. Even here, just as in the lifetime of an immunized individual, the immunity tends to fade out after a short time.

As a matter of fact, many of the instances that have been advanced to show the inheritance of acquired characters are simply transient hold-over somatic effects that have gained no permanent grip upon the hereditary stream of germplasm, and which consequently soon fade away.

In a similar way the gradual acclimatization of the mold, *Penicillium,* to a salt solution of a density sufficient to cause its death if the organism is placed in the solution at once, has been effected, and the resulting spores have produced molds that are able to survive in the concentrated solution. Here, of course, the spores have been acclimatized as well as the parent plant and it was to be expected that these spores would develop into molds habituated to the increased saline environment. This, however, is pseudo-heredity, for no permanent method of response has been established.

f. Prenatal Influences

Perhaps the most illogical and at the same time the most widespread of all types of supposed transmission of acquired characters are so-called "maternal impressions." The prevalence of this superstition has caused expectant mothers untold needless misery.

Popenoe and Johnson,[1] after an excellent and extended discussion of the matter, conclude as follows:

"To recapitulate, the facts are—

(1) That there is, before birth, no connection between the mother and child by which impressions made on the mother's mind or body could be transmitted to the child's mind or body.

(2) That in most cases the marks or defects whose origin is attributed to maternal impression, must necessarily have

[1] "Applied Eugenics."

been complete long before the incident occurred which the mother, after the child's birth, ascribes as the cause.

(3) That these phenomena usually do not occur when they are, and by hypothesis ought to be, expected. The explanations are found after the event, and that is regarded as causation which is really coincidence.

. . . . . .

It is easily understandable that any event which makes such an impression on the mother as to affect her health, might so disturb the normal functioning of her body that her child would be badly nourished, or even poisoned. Such facts undoubtedly form the basis on which the airy fabric of prenatal culture was reared by those who lived before the days of scientific biology."

C. THE GERMPLASM THEORY SUFFICIENT TO ACCOUNT FOR THE FACTS OF HEREDITY

Weismann holds that the theory of the continuity of the germplasm, already considered in a previous chapter, is sufficient in itself to account for the facts of heredity. Hence it is quite unnecessary to fall back upon the inheritance of acquired characters as an explanation, since this theory is at least difficult, if not impossible, of satisfactory proof.

To prove the inheritance of acquired characters, according to Weismann three things are necessary: *first,* a particular somatic character must be called forth by a known external cause; *second,* it must be something new or different from what was already exhibited before, and not be simply the reawakening of a latent germinal character; and *third,* the same particular character must reappear in succeeding generations in the absence of the original external cause which brought forth the character in question. As yet these condi-

tions have not been convincingly met in the evidence brought forward in support of the inheritance of acquired characters.

11. The Comparative Independence of Germ and Soma

The fact that the germ is only a pilgrim stranger passing through the homeless land of the soma is well brought out by the critical ovarian-transplantation experiments of Castle and Phillips upon guinea pigs.

The ovaries of an albino guinea pig were removed and

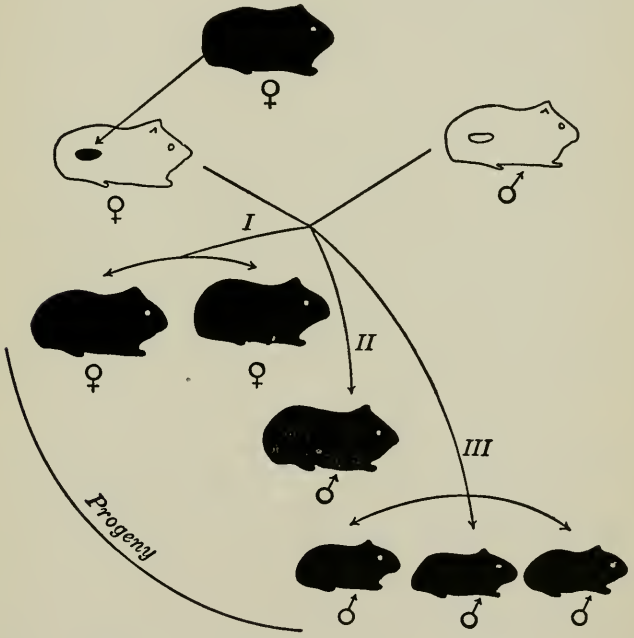

Fig. 12.—Diagram of ovarian transplantation experiment to show the influence of somatoplasm upon germplasm. Black is dominant over albino. The ovaries from a black guinea pig were engrafted into a female albino whose ovaries had been removed. Upon recovery this female was crossed three times with an albino male. All the progeny were black. Data from Castle and Phillips.

those of a black guinea pig were grafted in their place. After successful recovery from the operation the animal was mated with an albino male three times before pneumonia unfortunately put an end to this famous experiment. The resulting six offspring were all black, as shown in Figure 12. Ordinarily when albinos are crossed they produce only albinos. It is obvious that the pneumonia victim was not the mother of the six black offspring, although she bore them. "The conclusion is forced upon us," to quote Babcock and Clausen's comments on the case, "that the egg-cell during its growth does not change in germinal constitution. Its growth is like the growth of a parasite or of a wholly independent organism; what it takes up serves as food; this is not incorporated merely in the growing organism, it is *made over* into the same kind of living substance as composes the assimilating organism."

Heape likewise obtained albino rabbits following the transplantation of ovaries from albino rabbits into Belgian hares, and Davenport by similar transplantation experiments in poultry also demonstrated the failure of the parental soma to change the character of the germ-cells which it nourished.

12. Acquired Characters in the Protozoa

Although the problem of the inheritance of acquired characters is better defined among the higher animals where the distinction between the soma and the germ is more sharply cut than among the lower animals and plants, yet, as Jennings shows, one meets the same perplexities in the protozoa as in the metazoa. The difficulty in the inheritance of acquired characters is not so much in separating germ and soma as in the mechanism of cell-division. There seems to be no way in which an acquisition located at one end of a cell can overleap the barrier of cell division and appear at the other end after mitosis.

In his cultures Jennings found a *Paramecium* with an abnormal projection or spine at one end. This acquisition was handed on for five generations before it disappeared, but never in any generation did more than one of the offspring have

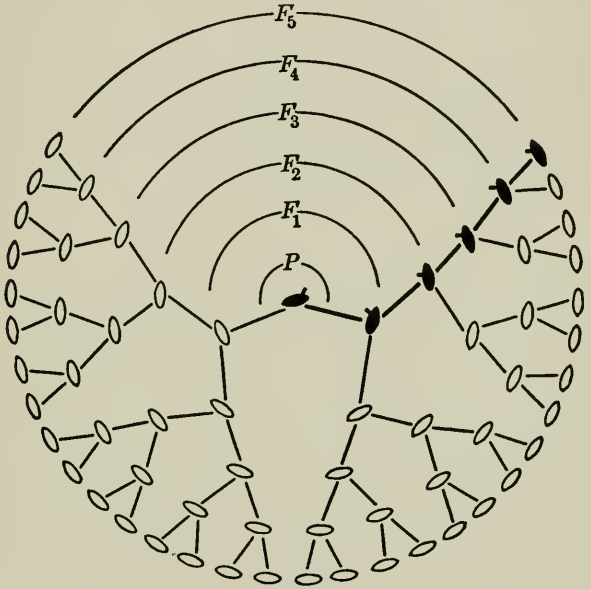

FIG. 13.—The behavior of an "acquired character,"—a spiny projection at one end of the body,—in the case of *Paramecium*. The original individual is represented in the center and its offspring, which arise by fission, are in successive circles. In the fifth generation only one out of 32 shows the spine. Data from Jennings.

the spine. In other words, it did not become hereditary although it continually reappeared in one individual in every generation. The reason for this will be apparent upon referring to Figure 13. The fission-half bearing the spine holds the same relation to the spineless half as soma to germ and there is here no mechanism for the transmission from one

half to the other. Simple transmission, like the persistence of the spine for five generations of *Paramecium,* is not heredity. The spine-bearer in the fifth generation carried the original spine which had been passed on like the wand in a relay race.

In order that a character shall be really inherited, that is, shall appear in more than one of the progeny and so affect the race, it must be *produced anew in each generation from a germinal determiner.* This is just as true for the protozoa as it is for the higher organisms.

13. The Opposition to Weismann

The opponents of Weismann point out, as a weak link in his argument, the assumption that the germplasm is so insulated from the somatoplasm as not to be influenced by it. Weismann assumes, of course, that the germplasm is isolated from the somatoplasm very early in the development of the fertilized egg into an individual, and that when once isolated it thereafter takes no active part in, nor is in any way affected by, the vicissitudes through which the somatoplasm, or the body itself, passes. The somatoplasm is thus merely a carrier of the germplasm and unable to affect the character of it any more than a rubber hot-water bag, although capable of assuming a variety of shapes, can affect the character of the water within it.

The possible independence of parts organically associated together as intimately as germplasm and somatoplasm, is shown also by the routine work of the orchardists whose grafts never take on the character of the host tree. Furthermore, the known behavior throughout synapsis and segregation of hereditary genes in Mendelian crosses, to be considered later, points unmistakably to the same possibility of close association, either

nutritive or otherwise, of two different organic substances without the one changing the character of the other thereby.

In opposition to this view it is urged that every organism is a physiological as well as a morphological unity, and that cells entirely insulated within such a unity would be a physiological miracle.

In this connection it must be remembered that nutritional dependence, without necessitating morphological modification to correspond with the source of the nutrition, is a fact commonly observed. Feeding a baby goat's milk does not result in a goat-like child.

There is abundant evidence that germ-cells, or rather certain hormones in the organs producing the germ-cells, do affect the somatoplasm under particular conditions, as, for example, in cases of castration when those somatic features called "secondary sexual characters" undergo profound modification. Even here, however, it must be pointed out that it is not the germ-cells themselves that are directly responsible for the modifications which occur, but rather the hormones of the interstitial gonadal cells.

A most serious fly in the Weismannian ointment is due to the results of certain experiments by Guyer and Smith.[1] These ingenious experimenters injected into fowls the freshly removed lenses of rabbits' eyes, pulped up in Ringer's solution. The fowls developed an "antibody" which tended to disintegrate the rabbit lenses. When serum from these fowls was in turn injected into pregnant rabbits the mother was unaffected, but nine out of sixty-one surviving young were born with degenerate eyes. The affected young carried the defect even in the male line through several generations without the injection of any more serum containing the lens antibody. "The

[1] Jour. Exp. Zoöl., III, 1920.

degenerating eyes are themselves, directly or indirectly, originating antibodies in the blood serum of their bearers—which in turn affect the germ-cells." If these conclusions are finally substantiated, the cardinal principle of the inheritance of acquired characters must be conceded to be possible. The end is not yet.

14. Various Results upon Offspring of Parental Acquisitions

In Fig. 14 an attempt is made to visualize the various results of parental acquisitions, both somatic and germinal, upon the generations following.

It will be noted that Case I, where the soma of the parent is represented as determining the soma of the offspring, is contrary to fact, for in sexual reproduction the offspring arises from the undifferentiated germplasm and not from the somatoplasm of its parents.

The usual result of a somatic modification is shown in Case II.

Pangenesis, Case III, postulates a reversal of the universal process of differentiation in that it demands a return of the elaborated soma with the modifications it has acquired during the course of its elaboration, to the primitive condition of the germ.

In Case IV the apparent inheritance of acquired characters is due not to the fact that the parental soma was modified, but because at the same time and in the same way that the parental soma was taking on a modification, the germ was likewise modified. This, to use the drug clerk's phraseology, is "something just as good" as the inheritance of acquired characters but it is not the Weismannian brand.

Finally, Case V shows a true mutation which occurs in the

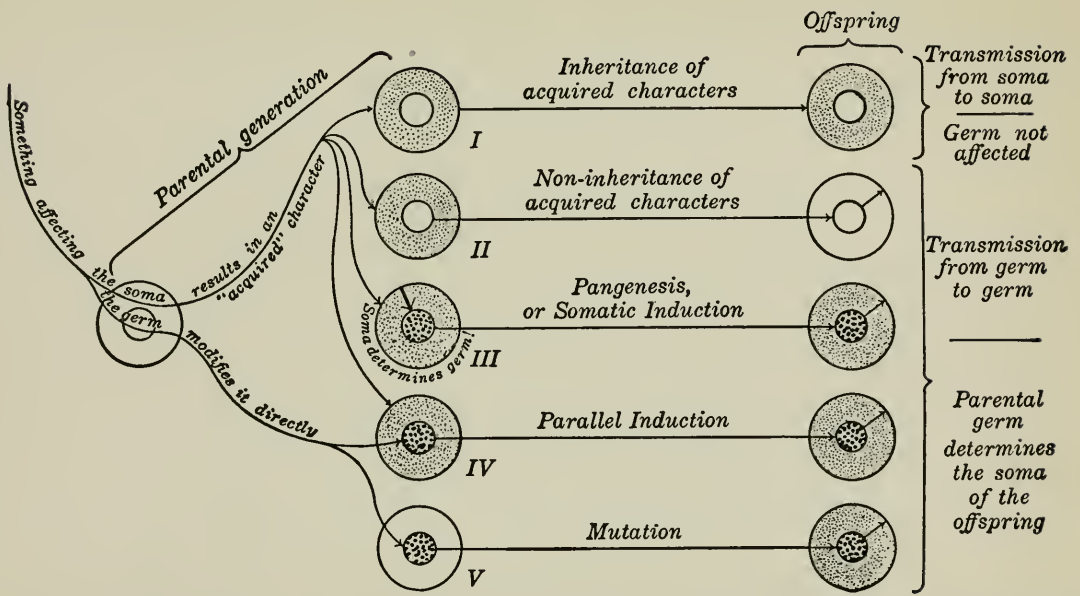

FIG. 14.—The theoretical results in the offspring, of parental acquisitions. The inner circles represent the germplasm contained within the somatoplasm, or larger circles. The course of transmission is shown by the arrows.

parental germplasm but does not appear to the light of day until the offspring develops.

15. Conclusion

Granting that the somatoplasm affects the germ-cells, the inheritance of acquired characters is by no means thereby established.

In order to do this, the precise acquired character in question, which indirectly exercised its influence upon the germ, must be redeveloped in the absence of the causes that brought about the original acquisition. Although the germplasm might conceivably receive an influence from the somatoplasm and be affected by it in a general way, it is a different matter entirely to develop anew the replica of the character itself that is supposed to have been acquired.

It will be seen in subsequent pages, under the discussion of data furnished by experimental breeding, that the weight of probability is decidedly against the time-honored belief in the inheritance of acquired characters, particularly as applied to the higher forms of life where the germplasm becomes more isolated from the somatoplasm.

If this conclusion seems to furnish a rather hopeless outlook for those who seek to control heredity, there remains the consolation suggested by J. Arthur Thomson's felicitous epigrammatic summary of the matter, "Although what is acquired may not be inherited, what is not inherited may be acquired."

CHAPTER V

MENDELISM

1. Methods of Studying Heredity

Modern studies in heredity have been pursued principally in three directions: first, by microscopical examination of the germ-cells; second, by statistical consideration of data bearing upon heredity; and third, by experimental breeding of animals and plants. In the present chapter attention will be directed to a consideration of experimental breeding with reference to hybridization, that is, breeding from unlike parents, a process which Jennings characterizes by the expressive phrase, "the melting-pot of cross-breeding."

2. The Melting-pot of Cross-breeding

Hybridization, or cross-breeding, as analyzed by Galton (1888), results in one of three kinds of inheritance, namely, blending, alternative, or particulate.

Of these, *blending inheritance* may be called the typical "melting-pot" in which contributions from the two parents fuse into something intermediate and different from that which was present in either parent. Galton illustrated this process by the inheritance of human stature in which a tall and a short parent produce offspring intermediate in height. A more detailed consideration of this type of inheritance will be presented in Chapter VIII.

By the method of *alternative inheritance* the parental con-

tributions do not blend upon union, but retain their individuality, reappearing intact in the offspring. In inheritance of human eye-color, for example, the offspring usually have eyes colored like those of one of the parents when the parental eye-color is unlike in the two cases, rather than eyes intermediate in color between those of both parents.

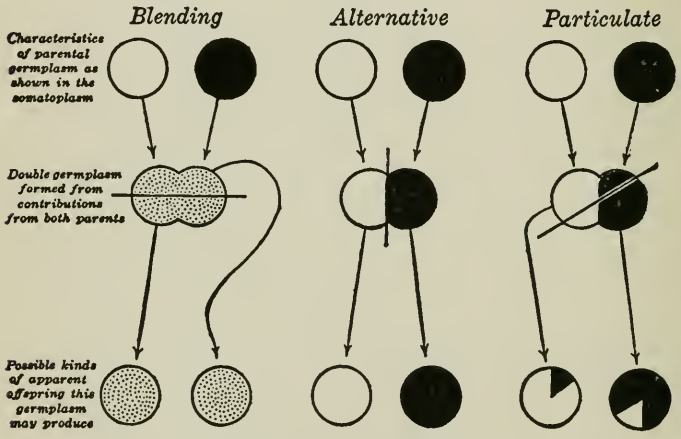
Blending
Alternative
Particulate
Characteristics of parental germplasm as shown in the somatoplasm
Double germplasm formed from contributions from both parents
Possible kinds of apparent offspring this germplasm may produce

FIG. 15.—Three kinds of inheritance described by Galton, when applied to a single pair of characters.

Particulate inheritance results when the offspring present a mosaic of the parental characters, that is, when parts of both the maternal and paternal characters reappear in the offspring without losing their identities by blending or without excluding one another. Piebald races of mice arising from parents with solid but different colors, or the black and white mosaic fowls produced from White Leghorns and Black Cochin bantams, may be cited as illustrations of this sort of inheritance, although it will be seen later in connection with the "factor hypothesis" that another interpretation of this phenomenon is not only possible but probable.

The distinctions between these three categories of inheritance are diagrammatically represented in Figure 15. A hybrid animal or plant may present among its various characteristics examples of all of these types of inheritance.

3. Gregor Johann Mendel

Our understanding of the working of inheritance in hybridization we owe largely to the unpretentious studies of an Austrian monk, Gregor Johann Mendel (1822-1884), who, although a contemporary of Darwin, was probably unknown to him. Bateson says of Mendel: "Untroubled by any itch to make potatoes larger or bread cheaper he set himself in the quiet of a cloister garden to find out the laws of hybridity, and so struck a mine of truth, inexhaustible in brilliancy and profit." For eight years Mendel carried on original experiments by breeding peas and then sent the results of his work for appreciation and publication to a former teacher, the celebrated Karl Nägeli, of the University of Vienna. At the time Nägeli's head was full of other matters, so that he failed to see the significance of his former pupil's efforts. However, in 1866 Mendel's results finally appeared in the Transactions of the Natural History Society of Brünn,[1] an obscure publication that reached hardly more than a local public. Here Mendel's investigations were buried, so to speak, because the time was not ripe for a general appreciation or evaluation of his work.

At that time neither the chromosome theory nor the germplasm theory had been formulated. Moreover, much of our present knowledge of cell structure and behavior was not even in existence. Weismann had not yet led out the biologi-

[1] "Versuche über Pflanzen-Hybriden." Verhandlungen naturf. Verein in Brünn. Abhandl. IV, 1865 (which appeared in 1866).

cal children of Israel through the wilderness upon that notable pilgrimage of fruitful controversy which occupied the last two decades of the nineteenth century, while the attention of the entire thinking world was being monopolized by the newly published epoch-making work of Charles Darwin.

Mendel died in 1884 unrecognized, and his work slumbered on until it was independently discovered, almost simultaneously, by three botanists whose researches had meanwhile been leading up to conclusions very much like his own. These three men were deVries of Holland, von Tschermak of Austria, and Correns of Germany. Their contributions were published only a few months apart in 1900 and were closely followed by important papers extending Mendelism to animals, from Bateson in England, Cuénot in France, and Castle and Davenport in America, with a rapidly increasing number from other biologists the world over. To-day the literature upon this subject has grown to be very large, and the end is by no means yet in sight.

Castle has well said: "Mendel had an analytical mind of the first order which enabled him to plan and carry through successfully the most original and instructive series of studies in heredity ever executed."

4. Mendel's Experiments on Garden Peas

What Mendel did was to hybridize certain varieties of garden peas and keep an *exact record of all the progeny,* in itself a simple process but one that had never been faithfully carried out by any one.

Earlier hybridizers fell short because they took for their basic unit the individual as a whole. Mendel's unit was a characteristic rather than an individual.

"To Mendel's foresight in arranging the conditions of his

work, as much as to his astuteness in interpreting the data, is due his remarkable success." (Morgan).

Before examining Mendel's results it may be well to state the difference between normal self-fertilization and artificial hybridization. Self-fertilization occurs when from the pollen and ovule of the same flower are derived the two gametes which uniting produce a zygote that develops into the seed and subsequently into the adult plant of the next generation. Peas, being self-fertilized, are never natural hybrids. In artificially crossing normally self-fertilized flowers it is necessary to carefully remove the stamens from one flower while its pollen is still immature, and later, at the proper time, to transfer to it ripe pollen from another flower.

Mendel's cross-breeding experiments on peas showed certain numerical relations among the progeny which gave rise to what has come to be rather indefinitely known as "Mendelism," and which may be temporarily formulated as follows:

When parents that are unlike with respect to any character are crossed, ordinarily the hybrid progeny of the first generation will apparently be like one of the parents with respect to the character in question.

Mendel termed the character that remains apparent in such a hybrid, the *dominant,* and the latent character which recedes from view, the *recessive.*

When, however, the hybrid offspring of this first generation are in turn crossed with each other, they will produce a mixed progeny, 25 per cent of which are like the dominant grandparent, 25 per cent like the other or recessive grandparent, and 50 per cent like the parents that resemble the dominant grandparent.

An illustration will serve to make plain the manner in which this rule works out. Mendel found that when peas of a

tall variety were artificially crossed with those of a dwarf variety, all the resulting offspring were tall like the first parent. It made no difference which parent was selected as the tall one. The result was the same in either case, showing that the character of tallness is independent of sex.

When these tall cross-bred offspring were subsequently crossed with each other, or allowed to produce offspring by self-fertilization, which amounts to the same thing, 787 plants of the tall variety and 277 of the dwarf kind were actually obtained by Mendel, making approximately the proportion of 3 to 1.

On further breeding the dwarf peas thus derived proved to be pure, producing only dwarf peas, while the tall ones were of two kinds, one-third of them "pure," breeding true like their tall grandparent, and two-thirds of them "hybrid" like their parents, giving in turn the proportion of three tall to one dwarf when interbred.

These crosses may be expressed as follows:

$$\text{Tall, } T, \times \text{ dwarf, } t, = \text{tall, } T(t).$$

That is, tallness crossed with dwarfness equals tallness with the dwarf character present but latent.

The members of such a Mendelian pair, as tall and dwarf, are termed *allelomorphs.*

If the hybrids, $T(t)$, are now crossed together, the result, algebraically expressed, is, as Mendel demonstrated, as follows:

$$\begin{array}{l} T + t \text{ (all possible egg characters)} \\ T + t \text{ (all possible sperm characters)} \\ \hline TT + \quad Tt \\ \qquad\quad Tt \quad + tt \\ \hline TT + 2\,T(t) + tt \end{array}$$

That is, one of the four possible cases is dwarf, *tt,* in character and the other three are apparently tall, although only one out of the three is pure tall, *TT,* while the remaining two are tall with the dwarf character latent, *T*(*t*).

The same thing may be expressed more graphically by the checkerboard plan, suggested by Punnett (Fig. 16). Each square of the checkerboard represents a zygote which, having received a gamete from each of the two parents, may develop into a possible offspring. The character of the gametes of the parents is shown outside of these squares, while the arrows represent the parental source from which the offspring have received their hereditary composition.

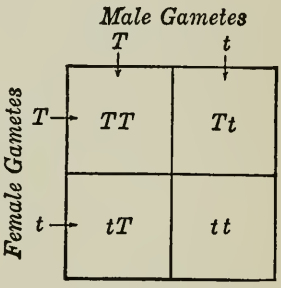

Fig. 16.—Diagram to illustrate theoretically the formation of the four possible zygotes in the second filial generation of a monohybrid.

The essential feature of Mendelism is briefly this: *hereditary characters are usually independent units which segregate out upon crossing, regardless of temporary dominance.*

Mendel carried on further experiments with garden peas,

Character	Number of Dominants	Number of Recessives	Ratio
Form of seed	5474 smooth	1850 wrinkled	2.96 to 1
Color of cotyledons . . .	6022 yellow	2001 green	3.01 to 1
Length of stem	787 tall	277 dwarf	2.84 to 1
Color of flowers	705 colored	224 white	3.15 to 1
Position of flowers . . .	651 axial	207 terminal	3.14 to 1
Form of pods	882 inflated	299 constricted	2.95 to 1
Color of unripe pods . . .	428 green	152 yellow	2.82 to 1
Total	14949	5010	2.98 to 1

using other characters. He obtained practically the same result as in the instance already given, for the actual progeny in the second generation of the cross-bred offspring figured up, as seen in the table on page 99, very nearly to the expected theoretical ratio of 3 to 1.

These general results have been confirmed by other investigators, for example, the yellow-green cotyledon-color cross has been repeated by Correns, Tschermak, Hurst, Bateson, Lock, Darbishire and White, with results totaling 195,477 in the second generation, of which number 146,802 were yellow and 48,675 were green. This is a proportion of 3.016 to 1, which is very close to the expectation of 3 to 1.

5. Some Further Instances of "Mendelism"

Since the rediscovery of Mendelism the ratio of 3 to 1 in the second hybrid generation has been found by a number of different investigators to be constant in a large array of characters observed both in animals and plants of diverse kinds when these are cross-bred with reference to the characters in question.

Botanists have some advantage perhaps in this matter of repeating and extending Mendel's conclusions, since they deal with forms which usually produce a large number of offspring from a single cross, a very desirable condition in establishing ratios. On the other hand, they are handicapped by being unable usually to obtain more than one generation in a year, while zoölogists may secure from animals like rabbits and mice several generations in a year, although unfortunately the number of progeny is ordinarily much smaller and the ratios obtained have a larger chance of error than is the case with the more numerous plant offspring.

What the modern experimenter in genetics desires is an

organism which first possesses conspicuous distinctive somatic characters, and, second, that will come to sexual maturity early and breed either in captivity or under cultivation, both numerously and frequently, with a minimum of trouble and expense.

Semi-microscopic animals, as, for example, the banana fly, *Drosophila,* which produces a large progeny every two weeks or so, may combine these general advantages, but they have the disadvantage of being so small that the detection of their distinctive phenotypic characters is attended with considerable technical difficulty.

The following table, compiled chiefly from Bateson [1] and

Organism	Author	Date	Dominant	Recessive
Nettle	Correns	'03	Serrated leaves	Smooth-margined leaves
Sunflower	Shull	'08	Branched habit	Unbranched habit
Cotton	Balls	'07	Colored lint	White lint
Snapdragon	Baur	'10	Red flowers	Non-red flowers
Wheat	Biffen	'05	Susceptibility to rust	Immunity to rust
Tomato	Price and Drinkard	'08	Two-celled fruit	Many-celled fruit
Maize	deVries	'00	Round, starchy kernel	Wrinkled, sugary kernel
Barley	vonTschermak	'01	Beardlessness	Beardedness
Silkworm	Toyama	'06	Yellow cocoon	White cocoon
Banana fly	Morgan	'10	Red eyes	White eyes
Land snail	Lang	'09	Unbanded shell	Banded shell
Salamander	Haecker	'08	Dark color	Light color
Canary	Bateson and Saunders	'02	Crest	Plain head
Poultry	Davenport	'06	Rumplessness	Long tail
Mouse	Darbishire	'02	Normal habit	Waltzing habit
Guinea pig	Castle	'03	Short hair	Angora hair
Cattle	Spillman	'06	Hornlessness	Horns
Horse	Bateson	'07	Trotting habit	Pacing habit
Man	Farrabee	'05	Brachydactyly	Normal joints

[1] "Mendel's Principles of Heredity," 1909.

Baur,[1] might now easily be much extended. It shows from what diverse sources confirmatory evidence of Mendelism had been derived within the first ten years of observation and experiment after its rediscovery.

6. The Cardinal Principle of Segregation

The essential thing which Mendel demonstrated was the fact that the determiners of heredity derived from diverse parental sources may unite in a common stream of germplasm from which, in subsequent generations, they may segregate out apparently unmodified by having been thus intimately associated with each other. This *law of segregation* depends upon the conception that the individual is made up of a bundle of determiners for all sorts of characteristics that are represented in the organism in question, each of which is present in double form since they are contributed by two parents. When a new individual originates from two parents by sexual reproduction, the two germ-cells involved, namely, the egg and the sperm, each eliminate one or the other of the determiners in every pair, thus leaving behind one complete set of determiners for the mature germ-cells in each case. The union of these two mature germ-cells with the reduced number of determiners restores the double set of determiners and forms the fertilized egg from which the new individual takes its rise. The capacity for segregation may be illustrated by the example of separate flowers picked from two gardens that, after having been made into a single nosegay, may again be taken apart and arranged without in any way disturbing the identity of the separate blossoms.

The general formula of Mendelism covering all cases of

[1] "Einführung in die experimentelle Vererbungslehre," 1911.

organisms cross-bred with respect to a single character, that is, *monohybrids,* is given in Figure 17.

The parents of a hybrid are usually referred to as the *parental generation* (P). The hybrid generation formed by crossing diverse characters in parents is designated as the *first filial generation* (F_1). The offspring of F_1 are F_2, and so on.

Incidentally this diagram hints how it is possible to derive

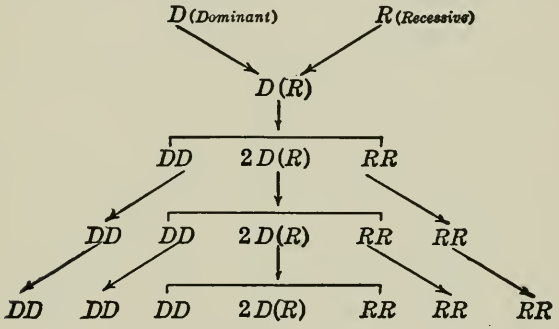

Fig. 17.—General Mendelian formula for a monohybrid.

a pure strain from an impure (hybrid) source, a fact of immediate interest not only to breeders of animals and plants but also to breeders of men. Such "extracted" recessives or dominants are entirely free from the hybrid impurity, and thus it is seen how contamination from hybridization may eventually be eliminated, just as a polluted stream may finally run pure.

7. Definitions

A character which is present in the offspring in double quantity because it was present in both parents is said by Bateson to be *homozygous.* An organism which is homozygous with

respect to any character is called a *homozygote* so far as that particular character is concerned (DD or RR).

In contrast to the homozygous condition, an organism is said to be *heterozygous* when it derives the determiner of a visible character from only one parent. Such an organism is described as a *heterozygote* or hybrid with respect to the character in question (DR).

Organisms that appear to be alike, regardless of their germinal constitution, are defined by Johannsen as identical *phenotypically* (DD and DR), while organisms having identical germinal determiners are said to be *genotypically* alike (DD and DD, or RR and RR).

The word "genotype" was suggested by Johannsen in honor of Darwin and his theory of pan*gen*esis, although there are certain objections to its use in this connection for the reason that systematists have already appropriated it for use in a different sense. As here used it signifies "the fundamental hereditary constitution or combination of genes of an organism" (Shull).

8. The Identification of a Heterozygote

"Homozygote" and "heterozygote" are terms descriptive solely of the genotypical constitution of organisms, and, as has been said, it is not always possible to distinguish one from the other by inspection.

One great service of Mendel was to show why it is that the appearance of an organism is not always a safe criterion for determining its genetic constitution and hereditary behavior. *The only sure way to identify a heterozygote is by breeding to a recessive and observing the kind of offspring produced.*

Peas of the formulæ TT and $T(t)$, for example, both look

alike, since a single determiner for the tall character, *T*, is sufficient to produce complete tallness. When, however, these two kinds of tall peas are each bred to a recessive dwarf pea, of the formula *tt*, the progeny will differ distinctly in the two cases as follows:

Case I. $T + T \times t + t =$ 100 per cent $T(t)$.
Case II. $T + t \times t + t =$ 50 per cent $T(t) +$ 50 per cent *tt*.

That is, if the dominant to be tested is homozygous (Case I), the entire progeny will exhibit the dominant character, but if the dominant to be tested is heterozygous (Case II), then only one-half of the progeny will show the character in question.

Sometimes when dominance is not pronounced it is possible to distinguish the heterozygotic dominant from the homozygotic dominant without resort to the breeding test. Correns has described an excellent instance of this type. When plants of a white-flowering race of the four-o'clock, *Mirabilis jalapa,* are crossed with those of a red-flowering race, all the offspring in the first filial generation, unlike either parent, exhibit rose-colored flowers. When, however, these rose-colored flowers are crossed with each other, they produce red, rose, and white in the Mendelian ratio of 1 : 2 : 1; that is, three colored to one white. The red-flowering race thus proves to be homozygous and the rose-flowering race heterozygous. Here color dominates the absence of color, or white, but the *degree* of the color depends upon whether the dose of color is double, from both parents, or single, from only one parent.

Altenburg says of this case: "The color of hybrid four-o'clocks might be compared to pink light which would result if lights from red and white lamps were thrown on a screen at the same time. In this case there is no mixing at the source;

the red and white lamps are themselves not changed. In the same way the red and white units in the four-o'clocks give rise to a mixed expression but the units themselves do not mix; otherwise the hybrid could not produce pure red and pure white offspring."

It should be repeated that in all instances it is not the factor of color, or any other characteristic, that is inherited, but a method of reaction or response to the environment that results in the color which has the same chemical basis in both parent and offspring.

9. The "Presence or Absence" Hypothesis

In place of Mendel's conception that every dominant character is paired with a recessive alternative or *allelomorph,* there has been proposed *the presence or absence hypothesis* which was first suggested by Correns but later logically worked out by others, particularly by Hurst, Bateson, and G. H. Shull. According to this interpretation, a determiner for any character either is, or is not, present. When it is present in two parents, then the offspring receive a double, or *duplex,* "dose," to use Hurst's word, of the determiner. When it is present in only one parent, then the offspring have a single, or *simplex,* dose of the character. When it is present in neither parent, it follows that it will not appear in the offspring. In this case the offspring are said to be *nulliplex* with respect to the character in question. Take the case of tall and dwarf peas, the determiner for tallness when present produces tall peas, even if it comes from only one parent, but if this determiner for tallness is absent from both parents, the offspring are nulliplex, that is, the absence of tallness results and only dwarf peas are produced.

The difference between the presence or absence hypothesis

and the dominant or recessive hypothesis of allelomorphs is that in the former case the "recessive" character has no existence at all, while in the latter instance it is present, but in a latent condition.

The reasons for and against the presence or absence interpretation may be more suitably considered later.

10. Dihybrids

So far reference has been made exclusively to *monohybrid individuals,* any two of which are supposed to be similar except with respect to a single unit character. Monohybrids are comparatively simple, but when two organisms are crossed which differ from each other with respect to *two* different unit characters, the situation becomes more complicated.

Mendel solved the problem of dihybrids by crossing wrinkled-green peas with smooth-yellow peas. He found that *smoothness* (S), is dominant over *wrinkledness* (W), and that *yellow color* (Y), is dominant over *green* (G), or, as it would be stated according to the presence or absence theory, smoothness is a positive character which fills out the seed-coat to plumpness while its absence leaves a wrinkled coat, and yellowness is a positive character due to a fading of the green which causes the yellow to be apparent. In the absence of this green-fading factor, or determiner, the green of course appears.

If smooth-yellow (SY), and wrinkled-green (WG), are crossed, all the offspring are phenotypically smooth-yellow, but they carry concealed the recessive determiners for wrinkledness and greenness according to the genotypic formula $S(W)Y(G)$. When the determiners of these cross-breds segregate out during the maturation of the germ-cells, they may recombine so as to form four possible double gametes, namely,

smooth-yellow (SY), and wrinkled-green (WG), that are exactly like the grandparental determiners from which they arose, and in addition, two entirely new combinations, smooth-green (SG), and wrinkled-yellow (WY).

Since the male and the female cross-breds are each furnished with these four possible gametic combinations; the total number of zygotes that may be formed by their union will be sixteen ($4 \times 4 = 16$). That is, the monohybrid proportion of 3 to 1 in dihybrid combinations is squared, $(3 + 1)^2 = 16$.

It of course does not follow that the offspring in dihybrid crosses will always be sixteen in number, or that they will always conform strictly to the theoretical expectation of $(3 + 1)^2$. The progeny obtained undoubtedly obey the laws of chance, but the greater the number of offspring, the nearer they come to falling into the expected grouping.

The sixteen possible zygotes resulting from a dihybrid cross may give rise to sixteen possible kinds of individuals which in turn, as will be demonstrated directly, present four kinds of phenotypic and nine kinds of genotypic constitutions.

A dihybrid mating, using the same symbols employed in the case just described, would be expressed algebraically as follows:

$$\begin{array}{llllll} SG+ & WY+ & SY+ & WG = \textit{all the possible egg gametes} & & \\ SG+ & WY+ & SY+ & WG = \textit{all the possible sperm gametes} & & \\ \hline SGSG+ & SGWY+ & SGSY+ & SGWG & & \\ & SGWY & & +WYWY+ & WYSY+ & WYWG \\ & & SGSY & & +\ WYSY & +SYSY+\ SYWG \\ & & & SGWG & +\ WYWG & +\ SYWG+WGWG \\ \hline SGSG+2SGWY+2SGSY+2SGWG+WYWY+2WYSY+2WYWG+SYSY+2SYWG+WGWG & & & & & \end{array}$$

The second and the ninth items in this result are genetically alike; by combining them the revised result reads:

$$SGSG+4SGWY+2SGSY+2SGWG+WYWY+2WYSY+2WYWG+SYSY+WGWG$$

There are then these nine different combinations of germinal characters or nine different genotypes in any dihybrid

cross. By placing the recessive characters in parentheses whenever the corresponding dominant is present, to indicate that the dominant causes the recessive to recede from view, these nine genotypes may be combined into four phenotypes as shown in the table below.

Phenotypes	9 *SY*	3 *SG*	3 *WY*	1 *WG*
Genotypes	4 *S(G)(W)Y* 2 *S(G)SY* 2 *SY(W)Y* *SYSY*	*SGSG* 2 *SG(W)G*	*WYWY* 2 *WYW(G)*	*WGWG*

From this analysis it may be said that the Mendelian ratio for a typical dihybrid is phenotypically 9 : 3 : 3 : 1, while that for a monohybrid, as we have already seen, is phenotypically 3: 1. This expected ratio corresponds essentially with the actual results which Mendel obtained in crossing smooth-yellow and wrinkled-green peas.

♂→ / ♀↓	*SG*	*WY*	*SY*	*WG*
SG	*SG* *SG* ①	*WY* *SG* ②	*SY* *SG* ③	*WG* *SG* ④
WY	*SG* *WY* ⑤	*WY* *WY* ⑥	*SY* *WY* ⑦	*WG* *WY* ⑧
SY	*SG* *SY* ⑨	*WY* *SY* ⑩	*SY* *SY* ⑪	*WG* *SY* ⑫
WG	*SG* *WG* ⑬	*WY* *WG* ⑭	*SY* *WG* ⑮	*WG* *WG* ⑯

FIG. 18.—Diagram to illustrate the possible combinations arising in the second filial generation (F_2) following a cross between yellow-smooth, *YS*, and green-wrinkled, *GW*, peas.

Figure 18 presents a graphic representation of the different combinations resulting from a dihybrid cross following the checkerboard plan used in Figure 16 to illustrate monohybrids.

The nine genotypes and four phenotypes which result from a dihybrid cross are shown in the following table:

Number in Each Class	Genotype	Number of Squares in Fig. 18	Phenotype	Number in Each Class
1	*SYSY*	11	*SY*	9
2	*(W)YSY*	7 · 10		
2	*S(G)SY*	3 · 9		
4	*S(G)(W)Y*	2 · 5 · 12 · 15		
1	*SGSG*	1	*SG*	3
2	*SG(W)G*	13 · 4		
1	*WYWY*	6	*WY*	3
2	*WYW(G)*	8 · 14		
1	*WGWG*	16	*WG*	1
16				16

Another illustration of dihybridism is shown in Figures 19 and 20 based upon data furnished by the Davenports.[1] In the matings given here, dark or pigmented hair, represented by solid black circles, is dominant over light-colored, that is, unpigmented or slightly pigmented hair, symbolized by open circles, while curly hair is dominant over straight, represented by crooked and straight lines respectively in the diagram. In other words, the presence of pigment is dominant over the absence of pigment, while the factor that causes

[1] "Heredity of Eye-color in Man," Science, N. S. 26, p. 589, 1907; "Heredity of Hair Form in Man," Amer. Nat. 42, p. 341, 1908. Davenport, C. B. and G. C.

curliness is dominant over the absence of this factor, with respect to human hair.

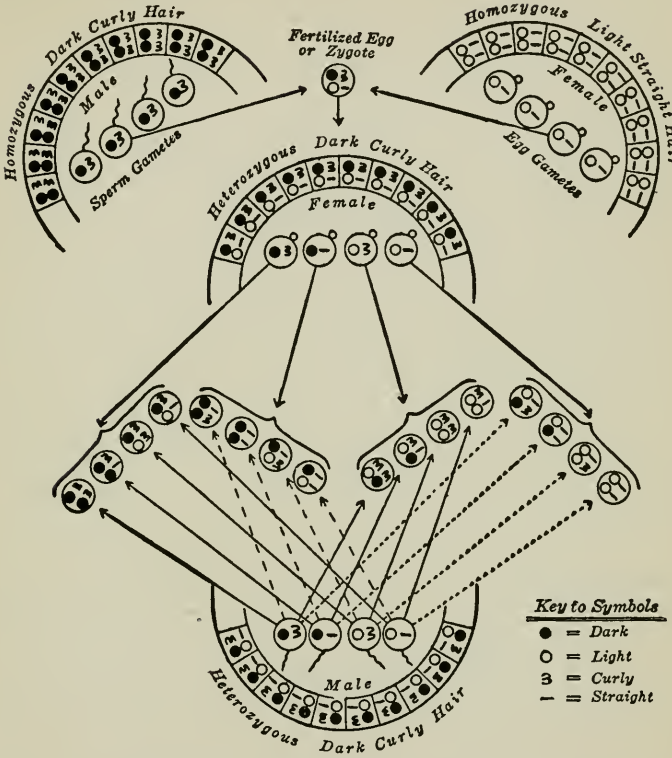

Fig. 19.—The heredity of human hair according to data by C. B. and G. C. Davenport. The arcs represent the somatoplasms of four individuals. Within the arcs are the gametes formed by these individuals. The dominant character is placed on the outside of the arc where it will be visible.

When a homozygous individual with dark curly hair crosses with a homozygous individual with light straight hair, all the offspring have dark curly hair.

The dark curly-haired individuals of this second (F_1) gen-

eration, however, are heterozygous with respect to each of these two hair characters. When any two individuals having this particular genotypic composition mate, therefore, they may produce any one of four possible phenotypes,—dark curly, dark straight, light curly, or light straight-haired individuals. These four phenotypes in turn will present nine different genotypic combinations out of sixteen possible cases, as shown in Figure 20.

Number in each class	Genotype	Phenotype	Number in each class
4		*Dark curly*	9
2			
2			
1			
1		*Dark straight*	3
2			
1		*Light curly*	3
2			
1		*Light straight*	1
16			16

Fig. 20.—Diagrams showing the possible genotypic and phenotypic combinations resulting when two heterozygous individuals with dark curly hair mate. Symbols are the same as in Figure 19.

Figure 19 serves furthermore to make clear: the distinction between somatoplasm and germplasm, the maturation of germ-cells, the segregation of gametes, and the formation of zygotes in sexual reproduction.

The cells of the somatoplasm are represented as making up the arcs within which are inclosed the germ-cells after their reduction through maturation, which results in giving in each germ-cell half the number of determiners that are present in the somatic cells.

It will be remembered that when two gametes, or mature germ-cells, unite, they form a zygote having the proper number of determiners normal to the species in question instead of double that number. Symbols for dominant characters in the diagram are placed on the *outside* of the somatic arcs,

because these are the characters that are visible or phenotypic, while the non-apparent recessives are placed on the inside out of sight.

11. The Case of the Trihybrid

Mendel went even further and computed the possibilities which would result when two parents were crossed differing from each other with respect to *three* unit characters. He found that the results actually obtained by breeding closely approximated the theoretical expectation.

This expectation in the case of a trihybrid cross is that the cross-breds resulting will all exhibit the three dominant characters, while their genotypic constitution will include six factors, namely, these three dominant characters plus their corresponding recessives or "absences."

Cross-breds of the first generation will, therefore, have eight possible kinds of triple gametes, and when interbred may form a possible range of sixty-four (8×8) different zygotes, which corresponds to a monohybrid raised to the third power $(3 + 1)^3$. These sixty-four zygotes group together in eight different phenotypes and twenty-seven different genotypes as shown on page 114.

The trihybrid cross with its resulting combinations is well illustrated by Castle's work on guinea pigs, which confirms the Mendelian hypothesis on an extensive scale. In Figure 21 dominant characters are represented by capital letters, while the allelomorphic recessives or absences are indicated by corresponding small letters.

When a smooth, or non-rosetted (r), *short-haired* (S), pigmented (P) guinea pig is crossed with a rosetted (R), long-haired (s), albino (p) guinea pig, all the offspring appear to be of one phenotypic constitution, namely, rosetted, short-

Number in each class	Genotype	Phenotype	Number in each class
1	*SS PP RR*	*SPR* Short, pigmented, rosetted	27
2	*SS Pp RR*		
2	*Ss PP RR*		
4	*Ss Pp RR*		
2	*SS PP Rr*		
4	*SS Pp Rr*		
4	*Ss PP Rr*		
8	*Ss Pp Rr*		
1	*SS pp RR*	*SpR* Short, albino, rosetted	9
2	*Ss pp RR*		
2	*SS pp Rr*		
4	*Ss pp Rr*		
1	*ss PP RR*	*sPR* Angora, pigmented, rosetted	9
2	*ss Pp RR*		
2	*ss PP Rr*		
4	*ss Pp Rr*		
1	*SS PP rr*	*SPr* Short, pigmented, non-rosetted	9
2	*SS Pp rr*		
2	*Ss PP rr*		
4	*Ss Pp rr*		
1	*ss pp RR*	*spR* Angora, albino, rosetted	3
2	*ss pp Rr*		
1	*SS pp rr*	*Spr* Short, albino, non-rosetted	3
2	*Ss pp rr*		
1	*ss PP rr*	*sPr* Angora, pigmented, non-rosetted	3
2	*ss Pp rr*		
1	*ss pp rr*	*spr* Angora, albino, non-rosetted	1
64			64

haired, and pigmented (*RSP*). Their genotypic constitution is represented by the formula *RrSsPp*. From these six factors may be formed eight possible triple gametes, as follows: *RSP, RsP, RSp, Rsp, rSP, rSp, rsP, rsp*. When two germ-cells each

♂ → / ♀ ↓	*RSP*	*RsP*	*RSp*	*Rsp*	*rSP*	*rsP*	*rSp*	*rsp*
RSP →	*RSP* *RSP*	*RsP* *RSP*	*RSp* *RSP*	*Rsp* *RSP*	*rSP* *RSP*	*rsP* *RSP*	*rSp* *RSP*	*rsp* *RSP*
RsP →	*RSP* *RsP*	*RsP* *RsP*	*RSp* *RsP*	*Rsp* *RsP*	*rSP* *RsP*	*rsP* *RsP*	*rSp* *RsP*	*rsp* *RsP*
RSp →	*RSP* *RSp*	*RsP* *RSp*	*RSp* *RSp*	*Rsp* *RSp*	*rSP* *RSp*	*rsP* *RSp*	*rSp* *RSp*	*rsp* *RSp*
Rsp →	*RSP* *Rsp*	*RsP* *Rsp*	*RSp* *Rsp*	*Rsp* *Rsp*	*rSP* *Rsp*	*rsP* *Rsp*	*rSp* *Rsp*	*rsp* *Rsp*
rSP →	*RSP* *rSP*	*RsP* *rSP*	*RSp* *rSP*	*Rsp* *rSP*	*rSP* *rSP*	*rsP* *rSP*	*rSp* *rSP*	*rsp* *rSP*
rsP →	*RSP* *rsP*	*RsP* *rsP*	*RSp* *rsP*	*Rsp* *rsP*	*rSP* *rsP*	*rsP* *rsP*	*rSp* *rsP*	*rsp* *rsP*
rSp →	*RSP* *rSp*	*RsP* *rSp*	*RSp* *rSp*	*Rsp* *rSp*	*rSP* *rSp*	*rsP* *rSp*	*rSp* *rSp*	*rsp* *rSp*
rsp →	*RSP* *rsp*	*RsP* *rsp*	*RSp* *rsp*	*Rsp* *rsp*	*rSP* *rsp*	*rsP* *rsp*	*rSp* *rsp*	*rsp* *rsp*

FIG. 21.—Diagram showing the possible combinations in a guinea pig trihybrid of the F_2 generation. *R*, rosetted coat; *r*, non-rosetted coat (absence of *R*); *S*, short hair; *s*, angora hair (absence of *S*); *P*, pigmented; *p*, albino (absence of pigment). The eight possible triple gametes of each parent are placed along the upper and left hand margins respectively. Each of the sixty-four squares represents a possible zygote or fertilized egg, having received a triple gamete from each parent.

made up of any one of these eight triple gametes unite in sexual reproduction, they will give rise to sixty-four (8×8) possible zygotes as displayed in Figure 21.

An analysis of Figure 21 shows among the offspring eight different phenotypes in the ratio of 27 : 9 : 9 : 9 : 3 : 3 : 3 : 1

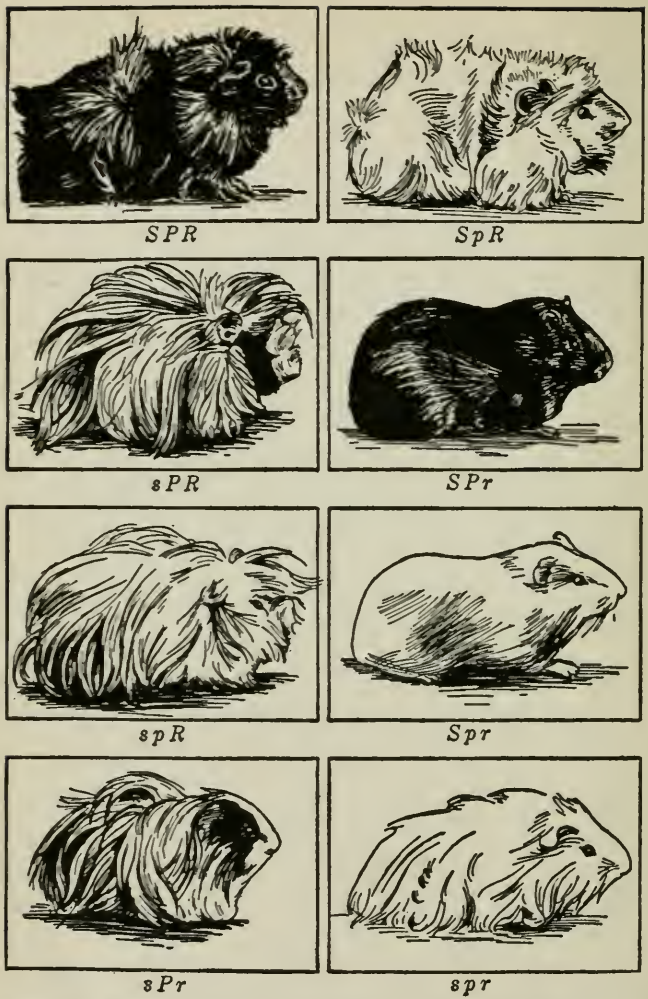

FIG. 22.—The eight phenotypically different kinds of guinea pigs in the F_2 generation of a trihybrid. S = short hair; s = long hair or angora; P = pigmented coat; p = non-pigmented coat or albino; R = rough or rosetted coat; r = smooth coat. Drawn from Castle's photographs by C. J. Fish.

and twenty-seven different genotypes in the proportions indicated on page 114. The *order* of the three pairs of symbols is changed from that in Figure 21 to emphasize the fact that with independent unit characters the order of their arrangement is immaterial.

Sketches, drawn from photographs in Castle's "Genetics and Eugenics," of the eight phenotypically different guinea pigs here described are shown in Figure 22.

The Mendelian expectation, following crosses involving different numbers of factors, is summarized below:

Number of Factor Pairs in which Parents Differ	Number of Different Phenotypes	Number of Different Genotypes	Number of Individuals Necessary to Obtain All of the Different Types
1	2	3	4
2	4	9	16
3	8	27	64
4	16	81	256
5	32	243	1024
6	64	729	4096
n	2^n	3^n	4^n

12. Summary

Three principles are primarily concerned in Mendelism, namely, independent assortment of hereditary determiners, dominance, and segregation.

a. Independent Assortment. An organism, although acting together as a physiological and morphological whole, may be regarded from the point of view of heredity as consisting of a large number of heritable unit characters which may recombine independently of each other.

b. Dominance. In every individual there are two determiners for every unit character, one derived from each parent. If this pair is different, *i. e.,* if the zygote is a heterozygote, one

dominates the other and determines the apparent character of the organism. Dominance implies nothing concerning the positiveness or negativeness of any character, but simply that a character can realize expression even in a heterozygote.

The alternative *recessive* characters, although they may be present in the germplasm, are unable to become manifest in the somatoplasm so long as the dominant characters are present. When, however, the dominant determiner is absent, and the recessive is duplicated, the recessive character becomes manifest. Recessiveness means that homozygosity is necessary for the expression of the character in question.

Dominance and recession, therefore, by making the analysis of hybrids possible, furnish a means for tracing the hereditary derivation of characters although of secondary importance in Mendelism.

c. Segregation. The diverse paired determiners of characters derived from the two parents, although they may be intimately associated together in the zygote during the complicated process of maturation that always precedes the formation of a new individual, retain their individuality and separate or segregate out uncontaminated by each other. They are thus enabled to unite into new combinations.

13. The Practical Application

Although the ratios for more complicated combinations than trihybrids were computed by Mendel, the experimental test was not carried out by him by breeding peas, since it involves such large and unwieldy proportions.

In the case of four differing unit characters in the parental generation, for example, the offspring of the tetrahybrids derived from such an ancestry would include 256 or $(3 + 1)^4$ possibilities instead of 64 or $(3 + 1)^3$, as in the case of trihy-

brids. When ten differing characters are combined in the parental generation, there would result over a million possible kinds of offspring among the hybrids of the second filial generation, $(3 + 1)^{10} = 1{,}048{,}576$.

From the foregoing it is apparent that in practical breeding the only hope lies in dealing with not more than one or two characters at a time. Since unit characters usually behave independently of each other, one may breed *for a single character* until it is segregated out in a homozygous, that is pure, condition, and then in the same way obtain a second character, a third, and so on.

This is not difficult if the character sought is a recessive, since in that case it is already homozygous or pure and consequently appears. When a character is dominant it takes longer to determine whether the individual is heterozygous (hybrid) or homozygous (pure).

14. Conclusion

The Mendelian method is an attempt to analyze the behavior of a particular characteristic in heredity rather than to get at the lump performance of the individual as a whole. Herein lies the scientific control of heredity which the trinity of Mendelian principles, namely, independent assortment, segregation, and dominance, has placed in human hands. Following this method there can be obtained in a few generations of properly directed crosses, combinations of characters united in one strain that formerly were never obtained at all or were only hit upon by the merest chance at long intervals.

Along with the elation, however, that comes with the acquisition of new stimulating knowledge in any field, it is well to recall the sage comment of that whimsical Hoosier philosopher, "Abe Martin," who says: "It's what we learn after we

think we know it all that counts," and as a timely warning to ambitious breeders who have great visions of the possibilities of practical accomplishment by means of the new tools of Mendelism. Bateson, with his customary caution, wisely says: "To prevent disappointment . . . it must at once be admitted that for fanciers Mendelism can as yet do comparatively little."

CHAPTER VI

THE PURE LINE AND SELECTION

1. Galton's Law of Regression

Galton was one of the first [1] to attempt to express mathematically the relationship between parents and offspring by means of treating statistically a single unit character. According to Galton, a mathematical expression of the correlation or relationship between two generations should serve as a cornerstone of heredity.

What Galton did was to take human stature as a unit character in comparing 204 English parents and their 928 adult offspring, because human stature is not complicated by environmental influences and is, consequently, a purely hereditary matter.

The results of his measurements expressed in inches are shown in Figure 23 in which the circles connected by the diagonal line represent the graded parental heights, while the arrowpoints indicate the average heights of the offspring in each group.

This illustrates Galton's *Law of Regression* or the tendency in successive generations toward mediocrity. The law may be stated as follows:

Average parents tend to produce average children; minus parents tend to produce minus children; plus parents tend to produce plus children; *but the progeny of extreme parents, whether plus or minus, inherit the parental peculiarities in a*

[1] "Hereditary Genius," 1869.

less marked degree than the latter were manifested in the parents themselves.

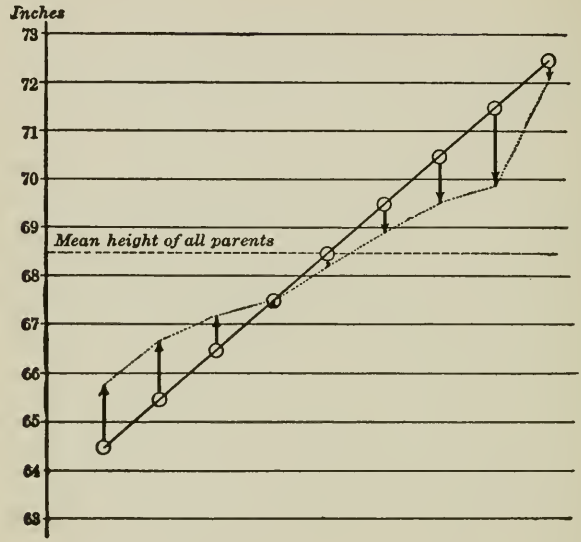

Fig. 23.—Scheme to illustrate *Galton's law of regression.* The circles represent graded groups of parental height while the arrowpoints indicate the average heights attained by the respective offspring. The offspring of undersized parents are taller, and of oversized parents are shorter than their respective parents. Based on data from Galton.

2. The Idea of the Pure Line

It was Galton's law of regression that suggested to the Danish botanist Johannsen (1857-1927) a possible means of controlling heredity. In his mind arose the question whether it would not be possible by continually breeding from plus parents, granting that plus parents produce plus offspring and making allowance for some regression to type, to shove over the offspring more and more into the plus territory and so to establish a plus race.

To test this hypothesis, Johannsen selected beans, *Phaseolus,* with which to experiment, since this group of plants is self-fertilizing, prolific, and easily measurable. Somewhat to his surprise, the beans refused to shove over as much as expected. That is, big beans did not yield principally big offspring, nor little beans little offspring, according to the expectation, although they each produced offspring that varied in the manner of fluctuating variability around an average unlike the parental type. This gave Johannsen the idea that he was using mixed material, so he next isolated the progeny of single beans, which, being self-fertilized for many generations, each constituted unmistakably a single hereditary line. In this way nineteen beans, now famous, became the known ancestors of Johannsen's original nineteen "pure lines," a further study of which has led the way to some of the most brilliant biological discoveries of recent years.

A pure line has been defined by Johannsen as "the descendants from a single homozygous organism exclusively propagating by self-fertilization," and still more briefly by Jennings as "all the progeny of a single self-fertilized individual."

It should be pointed out, however, that this technical idea of a pure line is not at all the same as that which the breeder has in mind when he uses the same term. The nearer individuals can be bred to conform to an arbitrary standard agreed upon, the better they illustrate the stock-breeder's idea of a "pure line." For example, in "The Standard of Perfection," a book published by the American Poultry Association, there are recognized 42 breeds and 121 varieties of chickens. To belong to any particular breed in this gallinaceous Blue Book the chicken must *look the part* regardless of its germinal derivation.

To the biologist, on the contrary, the pure line depends entirely upon similarity of the determining hereditary complex. The biologist's pure line is genotypic. The stock-breeder's is phenotypic, a difference of definition which has given rise to considerable confusion.

In a certain general way it will be seen that the pure line stands over against mutation, since it is concerned with the conservative maintenance of type while mutation attempts to change it.

The inevitable monotony of a pure line may be considerably masked by individual somatic modification. DeVries has said paradoxically, "The pure line is completely constant and extremely variable." That is, it is "completely constant" except for mutations, and it is "extremely variable" in the somatic development that may be attained by separate individuals.

3. Johannsen's Nineteen Beans

To return to experiments with beans, Johannsen found out that the progeny of every one of his pure lines varied around its own mean, which was different in each of the nineteen instances. When, however, extremes from any pure line series were selected and bred from, the results showed *complete regression* away from the extreme condition of the parent bean back to the type of the entire pure line in question. That is, *selection within a pure line is absolutely without effect* in modifying a particular character in the offspring of the line in question.

This is illustrated in Figure 24 in which the result of selecting for size in the year 1902 is shown for only four pure lines. The average for each pure line is given at the top of its column. When, for example, beans weighing 60 cg. were

selected from pure lines II, VII, and XV, the average weights of their progeny were 56.5, 48.2, and 45.0 cg. respectively, which in each instance is nearer to the average for the pure line than to the weight of the parental seed.

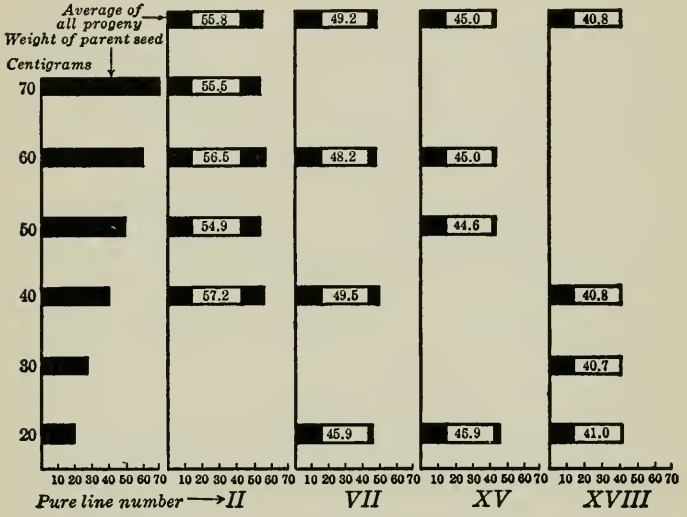

FIG. 24.—The result of selection in four pure lines of beans. The vertical columns, representing the average progeny from different-sized parents all derived from the same pure line, contain groups nearer alike than the horizontal columns, representing progeny from the same-sized parents, but different pure lines. All the numbers indicate centigrams. Data from Johannsen.

It will be seen at once that the averages in the vertical columns are nearer alike than the averages in the horizontal columns. In other words, the beans bred true to their pure line rather than to their fluctuating parent.

As a further example of this law, take the result of selection for six years in pure line I as shown in the accompanying table and in Figure 25.

Harvest Year	Mean Weight of Selected Parent Seed		Mean Weight of Offspring	
	Minus	Plus	From Minus Parent	From Plus Parent
1902	60	70	63.15	64.85
1903	55	80	75.19	70.88
1904	50	87	54.59	56.68
1905	43	73	63.55	63.64
1906	46	84	74.38	73.00
1907	56	81	69.07	67.66

It is evident, for instance, that in 1907 the smallest beans, weighing an average of 56 cg., gave an average progeny weighing 69.07 cg., while the largest ones for the same year, weighing an average of 81 cg., produced nearly the same average in their progeny as did the smallest beans, that is, 67.66 cg.

Incidentally all the progeny from both large and small parents averaged notably less in 1904 than all the progeny from large and small parents in 1906, a result due to a "poor year" when certain factors of environment were unfavorable. Such unfavorable conditions, however, are known to influence in no way the hereditary qualities of the beans. Thus it appears that, although the progeny of a pure line present plenty of variations of the fluctuating type, due probably to environmental differences in nutrition, moisture, etc., such variations are quite ineffectual so far as inheritance is concerned, and it makes no difference whether the largest or the smallest beans within a pure line are selected from which to breed, the result will be the same, in that there is a complete return to mediocrity or type with no "inheritance" of the parental modification. In fact, in 1903, 1906 and 1907 the lighter parents gave heavier progeny than the heavier parents.

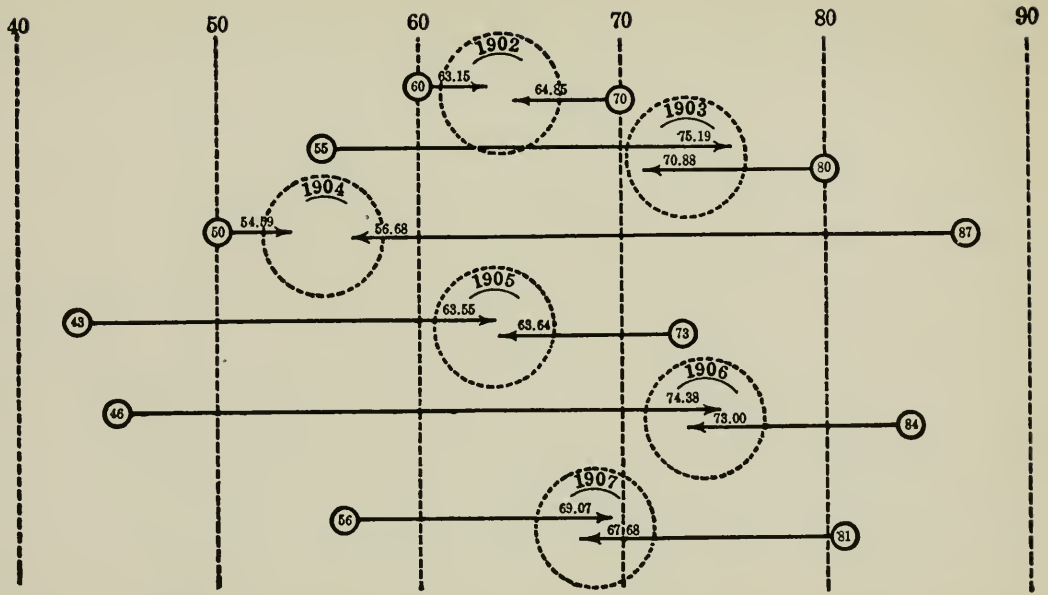

FIG. 25.—Diagram showing the negative result of selection for six years within "pure line 1" of Johannsen's beans. The small circles indicate the selected parents and the arrowpoints their respective progeny. In every case the weight of the average offspring is nearer the mean for the pure line than it is to that of its respective parent. Data from Johannsen.

It will be seen at once that here is a discovery of far-reaching importance which may require us to reconstruct certain cherished ideas about the part played in the evolution of species, as well as in heredity, by natural selection.

4. The Distinction between a Population and a Pure Line

A mixture of pure lines has been called a *population* (Johannsen).

It is not possible to distinguish by inspection a group of individuals composing a pure line from a group making up a population, since both may be phenotypically alike. Fluctuations about the average occur in both cases with no appreciable difference in character, although such fluctuations, when they occur within a pure line, are simply somatic differences caused in general probably by modifications in nutrition or some other external factor of environment, while fluctuations in a population include not only modifications of this transient nature, but also permanent hereditary differences due to germinal differences in the various pure lines of which the population is composed.

Johannsen has made the distinction between pure lines and populations clear by the following diagram (Fig. 26), in which five pure lines of beans are combined artificially to form a population.

The beans which make up the pure lines noted in this diagram are represented as inclosed within inverted test tubes. The beans in any single tube are all of one size. Tubes vertically superimposed upon each other also contain only beans of one size.

Thus it is seen that what may be a rare size of bean in one line, for instance that in the left-hand tube of *pure line 3,* may be identical with the commonest size in another line,

as *pure line 2*. The five pure lines represented in Figure 26 are combined in a *population* at the bottom of the diagram. In this population array the five pure lines are hidden.

Hence, while selection within a pure line has no hereditary influence, it is evident that selection within a population may shift or move over the type of the progeny obtained in the direction of the selection, simply by isolating a pure line of one type. Thus beans chosen from the extreme left-hand test tube in the population cited would belong only to *pure line 2*, while those taken from the extreme right-hand test tube could belong only to *pure line 3*.

Galton's "law of regression," namely, that minus parents give minus offspring

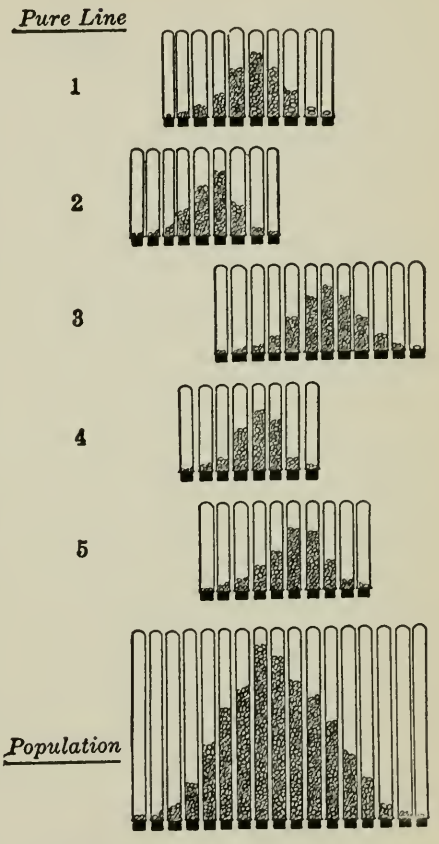

FIG. 26.—Diagrams showing five *pure lines* and a *population* formed by their union. The beans of each pure line are represented as assorted into inverted test tubes making a curve of fluctuating variability. Test tubes containing beans of the same weight are placed in the same vertical row. After Johannsen.

and plus parents plus offspring, with a tendency to reversion from generation to generation, depends simply upon a partial but not complete isolation of pure lines out of a population.

From this distinction between pure lines and populations it is clear why breeders in selecting for a particular character out of their stock need to keep on selecting continually in order to maintain a certain standard. As soon as they cease this vigilance, there is a "reversion to type" or, as they say, "the strain runs out," which means that the pure lines become lost in the mixed population which inevitably results as soon as selective isolation of the pure lines ceases.

Such reversion must always be the case in dealing with a population made up of a mixture of pure lines, for only by the isolation of pure lines can the constancy of a character be maintained. When, however, a pure line is once isolated, then all the members of it, large as well as small, are equally efficient in maintaining the pure line in question, regardless of their phenotypical constitutions.

Conceding that natural history and common usage as well as the older theories of heredity are concerned with phenotypic constitution of organisms, we are now coming to see more clearly than before that heredity must always be a case of *similarity in origin,* that is, in germinal composition, and that similarity in appearance by no means always indicates similarity in origin or true relationship.

The assumption that similarity in appearance does indicate relationship has been made the foundation of many conclusions in comparative anatomy and phylogeny, but to the modern student of genetics who places his faith in *things as they are,* rather than in *things as they seem to be,* conclusions based upon phenotypical distinction alone have in them a

large possible source of error which must be taken into account.

In a museum of heredity, should such an exhibit ever be assembled, the specimens would not be arranged phenotypically as they are in an ordinary museum where things that look alike are placed together as if in bonds of relationship, but they would be arranged *historically* from a genetic point of view to show their true serial origin one from another.

5. Cases Similar to Johannsen's Pure Lines

Although, according to Johannsen, pure lines are "the progeny of a single self-fertilized individual," it is plain that in at least three other possible categories something quite similar to "pure lines" may be obtained. These are *clones, parthenogenetic progeny* and *homozygous crosses.*

1. In asexual reproduction where the progeny are simply the result of continued fission of the original individual, a pure line may be said to continue from generation to generation because it is a germinally unchanged sequence of individuals. Such an asexual progeny is termed a *clone* (Webber) and it may be homozygous or heterozygous in character. Shull's definition of a clone is "a group of individuals of like genotypic constitution, traceable through asexual reproductions to a single ancestral zygote, or else perpetually asexual."

2. In cases of *parthenogenesis,* the progeny arising from a single female individual without the customary maturation of the germ-cells which accompanies typical sexual reproduction, constitute a pure line or an unmixed strain because as in clones there has been no segregation or mixture with outside germplasm.

3. In *homozygous crosses* when two organisms identical in their germinal determiners inbreed, their progeny will

form a pure line just as truly as do those of two parents that are united in a single hermaphroditic individual as the result of self-fertilization.

Morgan says, "In principle, pure lines, parthenogenetic reproduction and vegetative propagation are concerned with nearly the same situation."

In the case of clones and parthenogenesis it should be pointed out that the "pure line" is assured only so long as asexual reproduction continues. It is quite possible for an organism, even heterozygotic in composition, to continue to breed true or to produce an apparently pure line so long as asexual methods are employed. As soon as such an organism, however, changes to the sexual method of reproduction, segregation of characters may occur and different combinations result. A pure line, therefore, implies *freedom from admixture of different germplasm* rather than any necessary equality or likeness of individuals.

The different kinds of "pure lines" are diagrammatically represented in Figure 27.

6. Selection within a Pure Line

The basic idea of the pure line concept is that every member of any pure line is genetically identical with every other member of the same fraternity, therefore, any differences found between individuals of a pure line are entirely somatic and not hereditary.

The importance of the problem of pure line selection for any general consideration of the mechanism of evolution is at once apparent. There have been many recent investigations besides those of Johannsen to test the result of selection within the four kinds of "pure lines." Some of these investigations are cited in the table on pages 135 and 136.

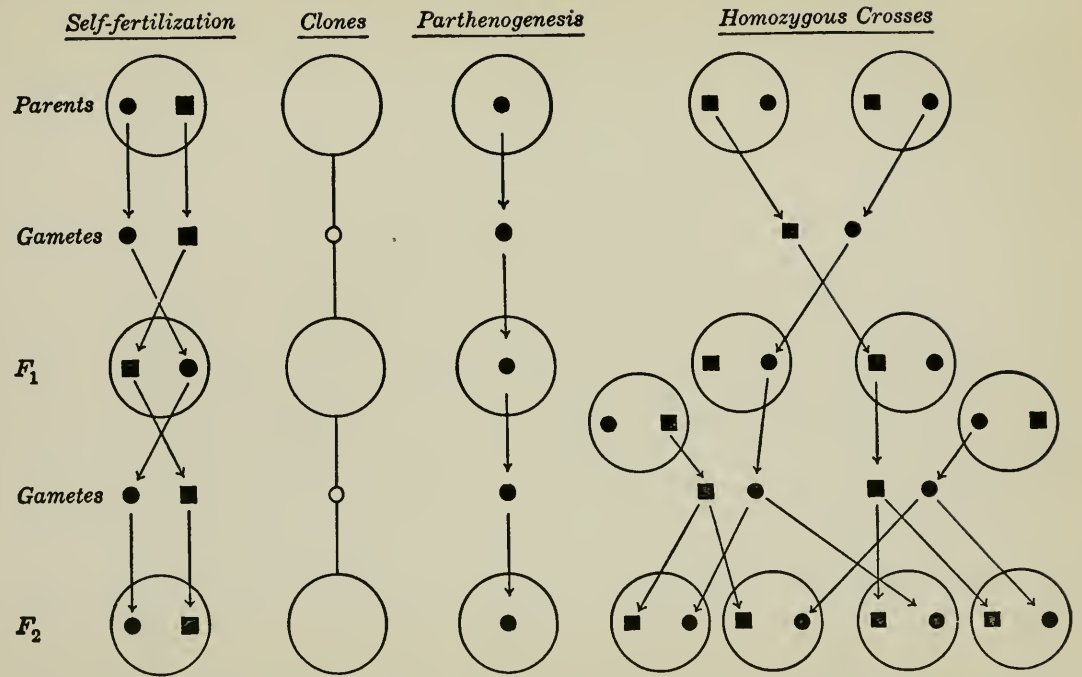

FIG. 27.—Different possible kinds of "pure lines." The black circles represent germplasm from the female and the squares the *same kind* of germplasm from the male.

It is apparent in the first section of the table that the pure line *sensu stricto,* that is, the pure line of Johannsen, must be studied with plants alone, since among animals only certain highly specialized parasitic worms, which do not lend themselves readily to selection experiments, produce offspring by means of self-fertilization. The work of the other authors upon plants, mentioned in the first group of the table is, in entire agreement with the work of Johannsen.

A. PROGENY OF A SELF-FERTILIZED PARENT

The noteworthy contribution of Henri de Vilmorin consists in a detailed comparison of preserved specimens of certain pure lines of wheat which were isolated in France about 1840, with their lineal descendants of to-day. In spite of continuous selection for betterment within these self-fertilized strains during more than 60 years, their constancy has been maintained.

B. CLONES

With respect to selection within a clone there is an apparent conflict of results.

With bacteria it is possible to isolate out variants from a single strain but in none of the cases is the origin of the supposed "clone" unquestionably *from a single bacterium* as it would need to be in order to form a true pure line.

Among the protozoa, which reproduce asexually by fission, painstaking experiments and many observations have been made, notably by Jennings and various investigators whom he has inspired.

For example, Jennings found that paramecia differ from each other in size, structure, physical character, and rate of multiplication as well as in the environmental conditions re-

quired for their existence and, furthermore, that these differences, in an hereditary sense, are "as rigid as iron."

THE RESULTS OF SELECTION WITHIN A PURE LINE

Kind of Pure Line	Author	Organism	Character Selected	Result
Progeny of a single self-fertilized individual	Johannsen, '03	Beans	Size	No effect
	"	Barley	Mealiness of kernel	" "
	Nilsson	Wheat Oats Barley	Various characters	" "
	Surface and Pearl, '15	Oats	Yield per acre	" "
	H. de Vilmorin	Wheat	Awns	" "
Clones	Wolf, '09	Bacteria	Pigment production	" "
	Meader, '19	"	Form, fermentative reaction. virulence	" "
	East, '09-'10	Potato		" "
	Vogler, '14	Garlic		" "
	Stout, '15	Coleus	Color pattern	Effective
	Mendiola, '19	Lemna	Size and shape of frond, speed of budding	No effect
	Jennings, '09	Paramecium	Size	" "
	" '16	Difflugia	Six shell characters	Effective
	Calkins and Gregory, '13	Paramecium	Size, rate of fission, etc.	"
	Jollos, '13	"	Resistance to arsenical poisoning	No effect
	Stocking, '15	"	Abnormalities	Effective in some lines
	Middleton, '18	Stylonychia	Fission-rate	Diverse strains from one
	Ackert, '16	Paramecium	Size	No effect
	Root, '18	Centropyxis	Shell characters, fission-rate	Effective
	Hegner, '19	Arcella	Shell characters	Diverse strains from one
	Hanel, '08	Hydra	No. of tentacles	No effect
	Lashley, '16	"	" " "	" "

THE RESULTS OF SELECTION WITHIN A PURE LINE—*Continued*

Kind of Pure Line	Author	Organism	Character Selected	Result
	Woltereck, '09	Hyalodaphnia	Length and shape of "head"	Temporary temperature effect
Parthenogenetic progeny	Ewing, '14	Aphids	Length of honeydew tubes, antennæ and body	" "
	Kelly, '13	"	Length of antennal joints	" "
	Banta, '19	Daphnids	Light reactions	Effective in one line
	" '19	Simocephalus	Sex intergrades	"Somewhat effective"
	Smith	Maize	Oil and protein content	Effective
	Tower, '06	Potato beetle	Pigmentation	No effect
	May, '17	Drosophila	Bar-eye	" "
	Zeleny, '20	"	"	Ineffective after 3 to 5 generations
Homozygous crosses	MacDowell, '15	"	Thoracic bristles	Effective
	Reeves, '16	"	Thoracic bristles	"
	Payne, '20	"	Thoracic bristles	Effective for several generations
	Sturtevant, '18	"	Dichaet bristles	Effective
	Pearl, '11	Hen	Fecundity	No effect
	Castle and Phillips, '14	Hooded rat	Coat pattern	Effective

With respect to the character of mean length he was able to isolate eight races, or pure lines, whose average size, drawn to scale, is shown in Figure 28.

Each of these pure lines produced a progeny that exhibited a considerable range of fluctuating variation. The offspring of *pure line D,* for example, varied from 256 to 80 micra [1]

[1] A micron is 1-1000th of a millimeter.

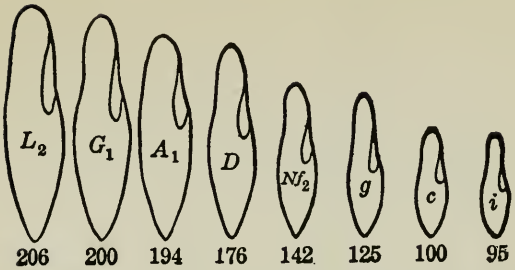

FIG. 28.—Eight pure races of *Paramecium*. The actual mean length of each race is given in micra below the corresponding outline. Magnified about 230 diameters. After Jennings.

in length with an average of 176 micra, as shown in Figure 29, where representative samples of the different classes of variants in *pure line D* are arranged in a series.

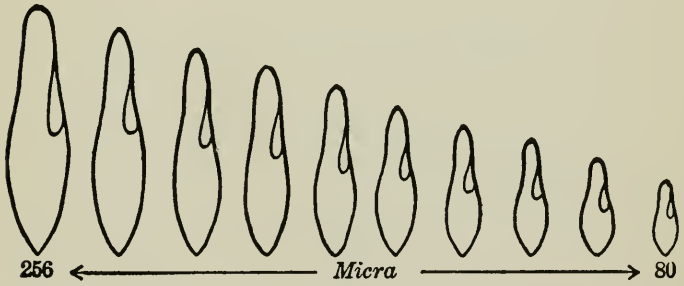

FIG. 29.—Diagram of a single race (*D*) showing the variation in the size of the individuals. Magnified about 230 diameters. After Jennings.

Representative sizes of each of the different classes of variants out of all the eight pure lines bred by Jennings are shown in Figure 30.

Each horizontal row represents a single race or pure line, the average size of which is indicated by the sign +. The

mean length of the entire lot, as shown by the vertical line, is 155 micra. The total number of individuals belonging to each size is not indicated, but in every horizontal line their number is more numerous near the average for that line and less numerous at the extremes, thus forming the typical normal frequency curves of fluctuating variability.

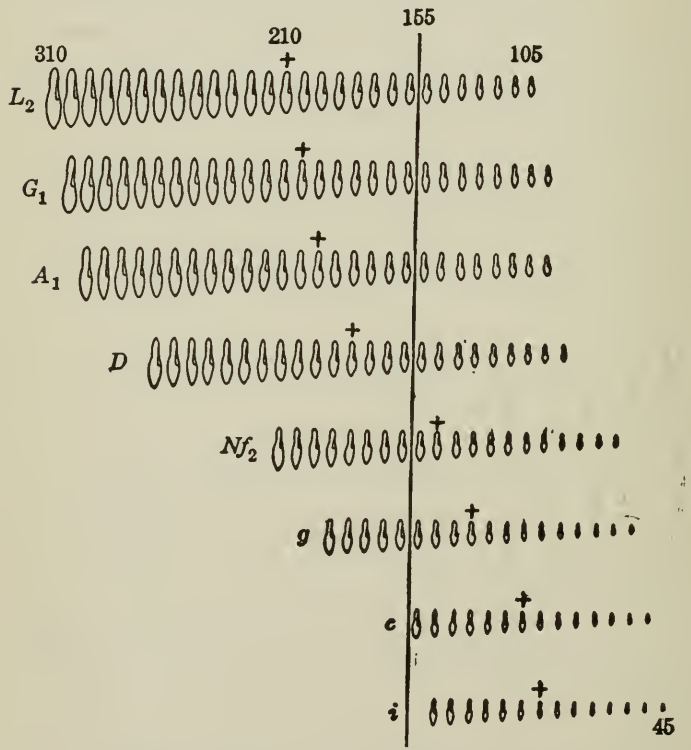

FIG. 30.—Diagram of the species *Paramecium* as made up of the eight different races, or pure lines, shown in Figure 28. Each horizontal row represents a single race. The individual showing the mean size in each race is indicated by a cross placed above it. The mean for the entire lot is at the vertical line. The magnification is about 24 diameters. After Jennings.

The significant fact about these series is that extreme individuals selected from any pure line do not reproduce extreme sizes like themselves, but instead, a progeny varying according to the laws of chance around the average standard of the particular line from which it came. Thus quite independently of Johannsen and working with an entirely different organism, Jennings arrived at the same general conclusion, namely, that selection within a pure line is without effect.

But with *Difflugia,* another protozoan that secretes for itself a jug-like shell, Jennings, after a careful and prolonged study, has a different story to tell. *Difflugia* proved to be a more favorable form to study than *Paramecium* because it has numerous distinctive shell characters which are all heritable to a high degree but are unchanged by growth and environment during the life of the individual, although presenting variations from parent to offspring.

Jennings selected for (1) the number of spines on the shell; (2) the length of the spines; (3) the diameter of the shell; (4) the depth of the shell; (5) the number of teeth surrounding the mouth; (6) the diameter of the mouth. In two families, "one (#303) including 495 descendants of a single individual, and the other (#314) including 1049 descendants of the original parent, selection was effective."

C. PARTHENOGENETIC PROGENY

Parthenogenetic animals furnish even better material than asexual clonal animals for testing the effectiveness of selection in an unmixed line but here again the conclusions of the investigators are not in entire harmony. There is no doubt that in most cases selection within a parthenogenetic line is futile, although Banta's long-continued observations upon Cladocera seem to furnish evidence of an opposite kind. Particular

weight should be given to this work because it presents one of the longest pure lines that ever passed under the seeing eye of a scientist. In some of his lines there have been, up to 1930, 964 generations forming an unbroken line extending over 19 years' time. If this pedigree were translated into human generations of 30 years each it would make a period of 28,920 years and would run back almost 300 centuries B. C., long before the very beginnings of human history. There is no doubt that many experiments in selection cannot be considered decisive because they concern altogether too few generations, as compared with the time that has been at the disposal of nature in accomplishing evolutionary change.

D. HOMOZYGOUS CROSSES

It is very difficult to find instances among animals and plants where two individuals are homozygous in all particulars. The nearest approach is "identical twins" which arise from a single fertilized egg and consequently are more nearly germinally alike, but they can never cross since they are always of the same sex.

It is useful, nevertheless, to consider pure lines resulting from homozygous crosses *when limited to a single character rather than to individuals,* for of this condition there are numberless instances. For example, two albino rabbits would furnish a pure line from a homozygous cross so far as albinism is concerned.

a. Tower's Potato-Beetles

As an illustration of the effect of selection within pure lines may be mentioned Tower's exhaustive experiments on the Colorado potato-beetle *Leptinotarsa decemlineata.* These beetles had been inbred for such an extended period that they

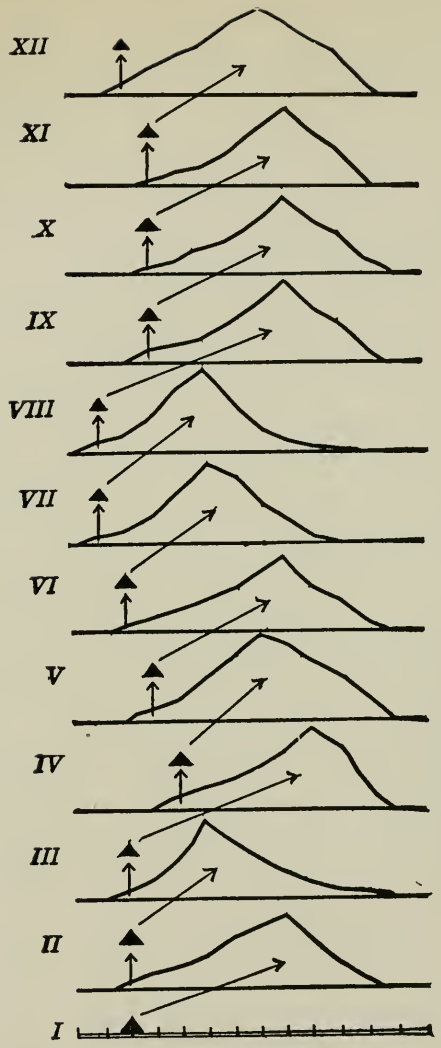

Fig 31.—Diagram showing the ineffectiveness of selection through twelve generations within a homozygous strain in the case of the Colorado potato-beetle (*Leptinotarsa*). In each generation extremely dark specimens were selected as the parents of the succeeding generation but the progeny always swung back to the type. After Tower.

were presumably homozygous for the character of color. Among the numerous cultures which were under control, a considerable variation in color, nevertheless, made its appearance. For convenience in classification these variations were graded into arbitrary classes or *graduated variants* ranging from dark to light.

When a male and a female from the extreme class at the dark end of the series were allowed to breed together, their progeny were not dark, but fluctuated in color around the original average of the entire series. The process of selecting each time an extreme pair of dark parents was continued for twelve generations, as shown in Figure 31, without in any way increasing the percentage of brunette potato-beetles in the progeny.

Thus in a pure line formed by the breeding of two individuals, alike with respect to color, the selection of an extreme variant was quite without effect in modifying the color of the progeny.

FIG. 32.—*Drosophila melanogaster*, the biological Cinderella. Drawn from Bridges by C. J. Fish.

b. Drosophila Bristles

Among the "hairs" on the scutellum of *Drosophila melanogaster* there are normally four larger hairs or bristles, as shown in Figure 32.

These four bristles are ordinarily strictly accounted for in heredity but the occasional variation in their number led MacDowell, and later others, to attempt to establish by selection a new style in these bristly decorations consisting of either extra or fewer bristles. Apparent success was the result of effective selection among the off-

spring of parents homozygous for the single character of four bristles.

c. Pearl's Egg-laying Hens

In an experiment extending over 17 years and which involved nearly 5000 pedigreed birds, Pearl tried, within a homozygous strain, to select a hen that would produce 200 eggs annually instead of the ordinary number of 125, but without success.

d. Castle's Hooded Rats

Finally one of the most famous selection experiments on record is that of extent of pigmentation, plus and minus, in the hooded rat. This experiment involved breeding an average of nearly twelve rats a day without cessation for eight years or a total of 33,249 and it has not only made the Pied Piper of Hamelin roll over in his grave but has kept biologists busy with explanations of the results, for, like the four bristles on *Drosophila's* back, it apparently furnishes evidence of modifications of an hereditary characteristic through selection following a presumably homozygous cross.

Castle succeeded in selecting two extreme races of rats from his hooded stock, one possessing almost no pigment and the other with the "hood" so extended that it covered practically the entire body. For a further consideration of this case see page 161.

Miss King selected rats for the ratio of the sexes, which is normally 105♂ to 100♀, and obtained ratios respectively 122♂ to 100♀ and 88♂ to 100♀.

7. Conclusion

Is the germ, then, a variable thing that makes it possible to select effective differences out of a pure line, to the discomfi-

ture of Mendelians who build their house on the rock of constancy of the germplasm, or can these perplexing results be otherwise explained?

At any rate it would be gratifying scientifically to discover one fundamental law to which all these various cases of pure line selection are accountable because intellectual satisfaction always follows upon finding the common denominator of things. Such a unifying explanation that makes a single harmonious interpretation of these apparently diverse results, based on the idea that all are reducible to Johannsen's conception of the *ineffectiveness of selection within a pure line,* has perhaps been reached in the *theory of modifying genes* which will be considered in the next chapter.

Certainly the pure line concept is a very useful tool for the geneticist, since with it the hereditary upset of outside germplasm is eliminated. Consequently it is of the utmost importance to know what can be done with this tool. In any event the way of experimentation and observation still lies open and what remains undiscovered makes life worth living.

CHAPTER VII

THE FACTOR HYPOTHESIS

1. The Hereditary Unit

In reducing any body of facts to a science, it is first necessary to determine the underlying units out of which the facts are made up.

Chemistry was alchemy until the chemical elements were identified and isolated. Histology was *terra obscura* until the cell theory brought forward "cells" as the units of tissues. In the same way there could be no science of genetics until the conception was developed that the individual is a bundle of separate characters rather than a unit in itself. So it has come about that geneticists speak of inheritance as applied to characters rather than to individuals as a whole.

The apparent somatic characters, like the color of the cotyledons or the length of the vine in Mendel's peas, are conditioned by intangible but nevertheless real germinal units, known as *genes* (Johannsen).

Mendel's experiments led him to believe that each somatic character depends upon a single determiner. He was apparently unaware that some characters may require many genes working together to bring them to somatic expression. The idea of compound germinal determiners for a single character, which has been repeatedly demonstrated during the past two decades, has come to be known as the *factor hypothesis* of heredity.

The factor hypothesis not only recognizes the fact that many separate genes may unite to determine a single somatic character, but also that a single gene in some instances may influence several diverse characters of the somatoplasm. For example, the determiner for gray hair in rats also produces lighter color on the belly, and the presence of the gene for melanic pigment may affect the color of very diverse organs in the body.

2. Different Kinds of Genes

There are various kinds of genes that act in different ways to bring about the visible expression of somatic characters.

When genes are derived from two parents, as in all cases of sexual reproduction, they are always in pairs or *allelomorphs,* that is, one from each parent. In the production of a somatic character either a single one or two or more allelomorphic pairs may take part.

If a single pair, the genes may be interpreted either according to the *alternative* conception or the *presence-or-absence* hypothesis. In the case of the pea-vine, for example, in the first instance it is either tallness or dwarfness. In the second instance, the determiner for the character of tallness either *is* present from one or both parents, or it *is not,* and the resulting somatic character is dependent on which of these two possibilities obtains. That is, if the hereditary gene for tallness is present the pea-vine will be tall, but if there is no gene for tallness the plant will be a dwarf. The manner of operation for such independent genes follows the typical Mendelian fashion described in Chapter V.

Among various kinds of plural determiners which involve more than one pair of genes, *duplicate genes* are those which are all alike qualitatively in their separate effects upon the

somatoplasm, but which, acting together, alter the degree of expression that is given to the character quantitatively. These will be more fully described in Chapter VIII upon "Blending Inheritance." It will be profitable in the present chapter to consider in some detail certain cases of plural determiners in which the genes modify each other qualitatively. They may be either *complementary,* when two or more factors, neither of which is effective alone, unite to produce a character; or *supplementary,* when a factor is added to a dissimilar one, already effective and patent, with the result that a character is modified or changed in some way.

Another type of determiners, that is of particular importance in solving some of the puzzles of heredity, are *lethal genes,* so-called since they "cause the early death of those gametes or zygotes in which such a factor is not balanced by a normal one" (Conklin).

3. Complementary Genes

In the course of numerous breeding experiments Bateson obtained two strains of white sweet peas, *Lathyrus,* which, when normally self-fertilized, each bred true to the white color. When these two strains were artificially crossed, however, the progeny all had purple flowers like the wild ancestral Sicilian type of all cultivated varieties of sweet peas.

Here was apparently a typical instance of "reversion" which would have delighted Darwin's heart, but according to the factor hypothesis the true explanation is as follows. The character of purple color is dependent upon two independent pairs of genes which, though separately heritable, are both required to produce it. Each of these white strains of sweet peas possesses one of these pairs of genes which can produce colored flowers only when united with its complement, a proof of

which appeared upon interbreeding hybrid purples from such a cross. In short, the color purple depends upon the action of two complementary genes that follow the behavior of a dihybrid. (See Chap. V, par. 10.)

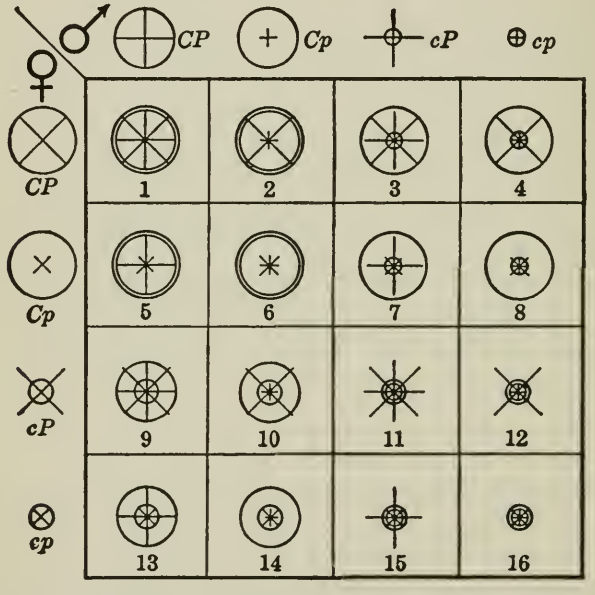

FIG. 33.—Diagram to illustrate the possible progeny from two heterozygous purple sweet peas, according to data from Bateson. *C*, color gene (large circles); *c*, absence of *C* (small circles); *P*, pigment gene (large crosses); *p*, absence of *P* (small crosses). In the zygotes within the checkerboard squares the gametic symbols are superimposed.

The formulæ for the two strains of white sweet peas used in this experiment are *CpCp* and *cPcP*, and the possible gametes that they can form are *Cp* and *cP*, respectively. *C* stands for a color gene, or chromogen, without which no color can appear, and *c* is the absence of this factor, while *P* represents a purple pigment gene, or activating enzyme, which finds ex-

pression in the somatoplasm only when taken together with the color gene *C*. The small letter *p* stands for the absence of the purple pigment gene. It will be seen that each of the white sweet peas, the formulæ of which are given above, lacks one of the two essential factors to produce the purple color. When the gametes from these two strains of white sweet peas are united, however, all the progeny are purple in color, with the formula *CpcP*.

These hybrid sweet peas upon gametic segregation theoretically produce four kinds of gametes, *CP, Cp, cP,* and *cp* which may combine, as any other dihybrid, in sixteen different ways. In this case, however, these combinations group themselves into only two phenotypes, purple and white, as indicated in the accompanying diagram (Fig. 33) in which *C* and *c* are represented by large and small circles respectively, while *P* and *p* are correspondingly indicated by large and small crosses. The gametic symbols are superimposed to form the zygotic patterns.

The theoretical expectation here shown was closely approximated in the actual results.

It may be noted in passing that the seven kinds of white sweet peas resulting from the above cross, while phenotypically alike, that is, in the zygotic symbols of Figure 33, lacking either the large circle (color) or the large cross (pigment), belong to three distinct groups of genotypes as follows:

		Number of Zygote in Figure 33
1	Without the pigment gene (large cross)	6 · 8 · 14
2	Without the color gene (large circle)	11 · 12 · 15
3	Without either pigment (large cross) or color (large circle)	16

Among the purple flowers are the following four genotypes:

		Number of Zygote in Figure 33
1	Duplex for both color (large circle) and pigment (large cross)	1
2	Duplex for color (large circle) but simplex for pigment (large cross)	2 · 5
3	Simplex for color (large circle) but duplex for pigment (large cross)	3 · 9
4	Simplex for both color (large circle) and pigment (large cross)	4 · 7 · 10 · 13

4. Supplementary Genes

a. castle's agouti guinea pigs

An illustration of a *supplementary gene* that acts only in conjunction with some other gene to bring about a modification, is the hair pattern determiner demonstrated by Castle in guinea pigs.

The wild gray *agouti* color of the hair of certain guinea pigs is due to the fact that pigment is distributed along the length of each hair in a definite pattern. The tip of a single hair is black followed by a band of yellow, while most of the proximal part which is more or less concealed by overlapping hairs is a leaden color. The distribution of pigment in such a pattern gives the characteristic gray, or "agouti," color to the coat when taken as a whole.

Castle demonstrated the separate nature and behavior of such a pattern gene when he discovered that it is transmitted *independently of pigment,* which is necessary to bring it to expression. He showed that upon crossing a solid black guinea pig, unquestionably possessing pigment but no "pattern," with a white albino guinea pig having no pigment, some of the off-

spring "reverted" to the ancestral agouti, or "pattern" type, thus proving that the pattern must be carried in this case by the white or albino guinea pig as a factor independent of the color necessary for its expression.

B. CUÉNOT'S SPOTTED MICE

Another instance of the interaction of supplementary genes is seen in the spotting of piebald mice. Cuénot discovered that such spotting is due to the absence of a *uniformity gene* which if present causes color to be uniformly distributed over the entire coat.

Both of these independent allelomorphic genes, spotting and uniformity, are real and not imaginary, since they may be separately transmitted through albino animals in the same way as the pattern gene mentioned above, notwithstanding that in albinos both are hidden through the absence of pigment, upon the presence of which their visibility depends.

Whenever piebald or spotted animals appear in a progeny derived originally from self-colored stock, it is evidently due to the absence of such a "uniformity" gene as has just been described.

Galton's theory of "particulate inheritance" (page 94) is now possibly explained as true alternative inheritance in which the mosaic appearance is caused by a Mendelian determiner, in this instance a spotting gene or, in other words, the absence of a gene for uniformity.

C. MISS DURHAM'S INTENSIFIED MICE

Miss Durham, in her work with mice, has demonstrated an *intensifying gene,* the absence of which she calls a *diluting gene.* The action of the former produces, as its name implies, intensity of color, while that of the latter serves to lessen the degree of intensity in which color appears.

These genes of intensity and diluteness, it should be observed, do not in any way correspond to the duplex and simplex condition of a dominant color character, either of which would straightway appear if crossed with an albino. The factors of intensity and dilution of color are of an entirely different nature, as they have been proven to be independently transmissible through albinos where a color character could not appear because of the absence of pigment.

The following illustration of this kind of supplementary genes taken from Miss Durham's experiments will serve to make the case clear. The symbols employed are:

B = *black* pigment which masks brown, or chocolate.
b = the absence of *B*, consequently *chocolate*.
I = intensity gene.
i = dilution gene or absence of intensity.
C = a complementary color gene acting with *P*.
P = a complementary pigment gene acting with *C*.
BICP = black.
BiCP = blue or maltese (dilute black).
bICP = chocolate.
biCP = silver-fawn (dilute chocolate).

The results of crossing the hybrids formed from the combinations indicated at the left in the table below are shown at the right where the expectation is given in parentheses after the actual results.

	Black (*BICP*)	Blue (*BiCP*)	Chocolate (*bICP*)	Silver-fawn (*biCP*)
Black (*BICP*) × Silver-fawn (*biCP*) . .	9(9)	4(3)	3(3)	2(1)
Blue (*BiCP*) × Chocolate (*bICP*) . .	42(45)	16(15)	14(15)	8(5)
Blue (*BiCP*) × Silver-fawn (*biCP*) . .	0(0)	33(36)	0(0)	12(12)

It will be seen that the actual results, even when such small totals are concerned, approximate very closely the expectation and are entirely consistent.

D. CASTLE'S BROWN-EYED YELLOW GUINEA PIGS

Furthermore Castle has shown that in guinea pigs there is an independent gene for *extension* of pigment distinct from the uniformity gene already mentioned. The absence of this extension gene (*restriction*) is manifested by a lack of black or brown pigment everywhere except in the eyes and to a slight extent in the skin of the extremities, *while the distribution of yellow is wholly unaffected by it.*

That such "extension" and "restriction" genes really exist, is proven in the following way.

When a brown (chocolate) guinea pig is crossed with an ordinary black-eyed yellow one, the young are all black pigmented, but by cross-breeding these hybrid young four varieties are obtained in the next generation, viz., black, brown, black-eyed yellow, and *brown-eyed yellow,* the latter a variety unknown before Castle's experiment in breeding was made.

For the sake of clearness the formation of the brown-eyed yellow is shown in Figure 34.

Symbols

B = *black* pigment, hiding brown or chocolate.
b = absence of B, or *chocolate.*
Y = yellow pigment, hidden by B.
E = extension of B over entire body, hiding Y.
e = restriction of B to eyes alone, thus exposing Y over the entire body.
C = complementary color gene acting with P to produce color.
P = complementary pigment gene acting with C to produce color.
(The genes C and P may be omitted for the sake of simplicity, since they are present in each instance.)

First Cross

"Extended" chocolate (*bbEEYY*) $\times$ black-eyed yellow (*BBeeYY*) = black (*BbEeYY*).

Second Cross

When these cross-bred blacks (*BbEeYY*) are mated with each other, they each form four kinds of gametes, *BEY, BeY,*

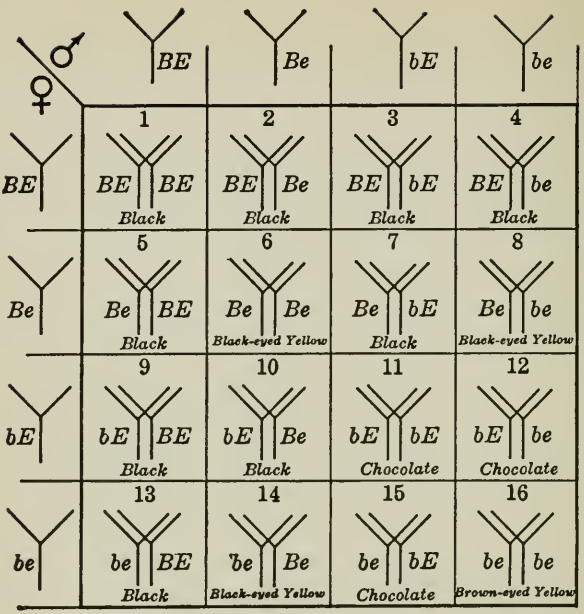

FIG. 34.—Diagram to illustrate the origin of a brown-eyed yellow guinea pig from two heterozygous black parents, based upon Castle's experiments. The gene for yellow (*Y*) is present in every gamete and is consequently duplex in every zygote but is hidden whenever the gene *B* is present. *B*, black pigment hiding brown or chocolate; *b*, chocolate (absence of *B*); *E*, extension of *B* over the entire body hiding *Y*; *e*, restriction of *B* to eyes alone thus exposing *Y* over the entire body.

bEY, and *beY*, which unite into sixteen theoretical zygotic possibilities, some of which are unlike (Fig. 34). These fall into four phenotypes, nine black (*BEY*), three black-eyed yellow (*BeY*), three chocolate (*bEY*), and one brown-eyed yellow (*beY*).

The actual results in Castle's experiments gave all four kinds in close numerical agreement with this expectation. The action of extension and restriction genes is, therefore, plainly

a case of Mendelian dihybridism in which two independent pairs of alternative characters are concerned.

E. RABBIT PHENOTYPES

Perhaps no better application of the factor hypothesis, so far as supplementary genes are concerned, may be found than in the case of the color of rabbits.

There are many varieties of rabbits with respect to color, particularly among domesticated races. These varieties are now quite explainable by the factor hypothesis, as indicated in the table below. The sixteen kinds of rabbits there catalogued have been obtained by Castle and other experimental breeders, as well as many of the albino types that would double this list if *c*, or the gene for absence of color, should be substituted for *C*, the presence of color, in column 4 of the table on page 156.

Explanation of Symbols in the Following Table

Br = a gene acting on *C* to produce *brown* pigmentation.

B = a gene acting on *C* to produce *black* pigmentation.

Y = a gene acting on *C* to produce *yellow* pigmentation.

The three genes, *Y, B, Br,* are present in every rabbit gamete and up to date have not been separable as independent unit characters, although they have been separated out in guinea pigs and mice. There are no brown rabbits, because black always goes linked with brown, thus covering the brown factor. Yellow rabbits result, as explained below, through the action of factor *e*.

C = a common *color* gene, or chromogen, necessary for the production of any pigment. It was discovered in 1903 by Cuénot.

c = the absence of *C* which results in albinos, regardless of whatever pigment gene may be present. By changing *C* to *c*, sixteen kinds of albinos would be added to this catalogue, an addition of one phenotype and sixteen genotypes, all looking alike but breeding differently.

E = a gene governing the *extension* of black and brown pigment, *but not of yellow*.

e = the absence of extension or *restriction* of black and brown pigment to eyes and the skin of the extremities only, while yellow remains extended and visible. Demonstrated by Castle in 1909.

I = an *intensity* gene which determines the degree of pigmentation. It can be transmitted independently of *C* through an albino. Discovered by Bateson and Durham in 1906.

i = the absence of intensity or *dilution*. Dilute black = blue. Dilute yellow = cream. Dilute gray = blue-gray.

U = a gene for uniformity of pigmentation or "self-color" discovered by Cuénot in 1904.

u = the absence of uniformity which results in *spotting with white*.

A = a pattern gene for agouti, or wild gray color, which causes the brown and black pigments to be excluded from certain portions of each hair, resulting in the gray coat. When present in the rabbit, it is also associated with white or lighter color on the under surfaces of the tail and belly. It was demonstrated by Castle in 1907.

a = the absence of agouti or pattern gene.

THE FACTOR HYPOTHESIS APPLIED TO COLORS OF RABBITS

CONSTANT GENES			ALTERNATIVE GENES					GAMETIC FORMULA	PHENOTYPIC CHARACTER WHEN CROSSED WITH THE SAME KIND OF GAMETIC COMBINATION
1	2	3	4	5	6	7	8		
						U	*A*	*AUIEC* [*YBBr*]	Gray
							a	*aUIEC* [*YBBr*]	Black
					I	*u*	*A*	*AuIEC* [*YBBr*]	Gray spotted
							a	*auIEC* [*YBBr*]	Black spotted
				E		*U*	*A*	*AUiEC* [*YBBr*]	Blue-gray
							a	*aUiEC* [*YBBr*]	Blue (Maltese)
					i	*u*	*A*	*AuiEC* [*YBBr*]	Blue-gray spotted
							a	*auiEC* [*YBBr*]	Blue spotted
Br	*B*	*Y*	*C*			*U*	*A*	*AUIeC* [*YBBr*]	Yellow (with white belly and tail)
					I		*a*	*aUIeC* [*YBBr*]	Sooty yellow (with yellow belly and tail)
						u	*A*	*AuIeC* [*YBBr*]	Yellow spotted
							a	*auIeC* [*YBBr*]	Sooty yellow spotted
				e		*U*	*A*	*AUieC* [*YBBr*]	Cream
					i		*a*	*aUieC* [*YBBr*]	Pale sooty yellow
						u	*A*	*AuieC* [*YBBr*]	Cream spotted
							a	*auieC* [*YBBr*]	Pale sooty yellow spotted

The Kinds of Gray Rabbits (Color only)

	Genotype Zygotic Formula	Number of Heterozygotic Factors	Phenotypes When inbred, these kinds are produced																					
			Gray	Black	Gray spotted	Black spotted	Blue gray	Blue	Blue gray spotted	Blue spotted	Yellow	Sooty	Yellow spotted	Sooty spotted	Cream	Pale sooty	Cream spotted	Pale sooty spotted	White
1	*AAUUIIEECC* [*YBBr*] [*YBBr*]	None	×																×
2	*AAUUIIEECc* [*YBBr*] [*YBBr*]	One	×																
3	*AAUUIIEeCC* [*YBBr*] [*YBBr*]	One	×								×								
4	*AAUUIiEECC* [*YBBr*] [*YBBr*]	One	×				×												
5	*AAUuIIEECC* [*YBBr*] [*YBBr*]	One	×		×														
6	*AaUUIIEECC* [*YBBr*] [*YBBr*]	One	×	×															
7	*AAUUIIEeCc* [*YBBr*] [*YBBr*]	Two	×								×								×
8	*AAUUIiEECc* [*YBBr*] [*YBBr*]	Two	×				×												×
9	*AAUuIIEECc* [*YBBr*] [*YBBr*]	Two	×		×														×
10	*AaUUIIEECc* [*YBBr*] [*YBBr*]	Two	×	×															×
11	*AAUUIiEeCC* [*YBBr*] [*YBBr*]	Two	×				×				×				×				
12	*AAUuIIEeCC* [*YBBr*] [*YBBr*]	Two	×		×						×		×						
13	*AaUUIIEeCC* [*YBBr*] [*YBBr*]	Two	×	×							×	×							
14	*AAUuIiEECC* [*YBBr*] [*YBBr*]	Two	×		×		×		×										
15	*AaUUIiEECC* [*YBBr*] [*YBBr*]	Two	×	×			×	×											
16	*AaUuIIEECC* [*YBBr*] [*YBBr*]	Two	×	×	×	×													
17	*AaUuIiEECC* [*YBBr*] [*YBBr*]	Three	×	×	×	×	×	×	×	×									
18	*AaUuIIEeCC* [*YBBr*] [*YBBr*]	Three	×	×	×	×					×	×	×	×					
19	*AaUuIIEECc* [*YBBr*] [*YBBr*]	Three	×	×	×	×													×
20	*AaUUIiEeCC* [*YBBr*] [*YBBr*]	Three	×	×			×	×			×	×			×	×			
21	*AaUUIiEECc* [*YBBr*] [*YBBr*]	Three	×	×			×	×											×
22	*AaUUIIEeCc* [*YBBr*] [*YBBr*]	Three	×	×							×	×							×
23	*AAUuIiEeCC* [*YBBr*] [*YBBr*]	Three	×		×		×		×		×		×		×		×		
24	*AAUuIIEeCc* [*YBBr*] [*YBBr*]	Three	×		×						×		×						×
25	*AAUuIiEECc* [*YBBr*] [*YBBr*]	Three	×		×		×		×										×
26	*AAUUIiEeCc* [*YBBr*] [*YBBr*]	Three	×				×				×				×				×
27	*AAUuIiEeCc* [*YBBr*] [*YBBr*]	Four	×		×		×		×		×		×		×		×		×
28	*AaUUIiEeCc* [*YBBr*] [*YBBr*]	Four	×	×			×	×			×	×			×	×			×
29	*AaUuIIEeCc* [*YBBr*] [*YBBr*]	Four	×	×	×	×					×	×	×	×					×
30	*AaUuIiEECc* [*YBBr*] [*YBBr*]	Four	×	×	×	×	×	×	×	×									×
31	*AaUuIiEeCC* [*YBBr*] [*YBBr*]	Four	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
32	*AaUuIiEeCc* [*YBBr*] [*YBBr*]	Five	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×

F. THE KINDS OF GRAY RABBITS

Each of the apparent kinds of gray rabbits indicated in the foregoing table may be made up of various genotypes. For instance, there are thirty-two different genotypes, each of which is phenotypically a gray rabbit. The zygotic formula for each of these thirty-two possibilities is displayed in the table on page 157, and it will be seen that these range all the way from rabbits homozygous in all their variable characters (No. 1) to those homozygous in none (No. 32).

The progeny of these various types of gray rabbits when inbred will consequently vary from the pure gray, as in No. 1, to a gray from which sixteen possible colored types of young may be expected as in No. 32.

Up to the time when Castle's paper upon the factor hypothesis[1] was published in 1909, nine genotypic kinds of gray rabbits had been obtained in his experiments, whose genotypic formulæ correspond to the following numbers in the list: 1, 3, 6, 10, 13, 20, 22, 28, 29.[2]

5. Lethal Genes

Among mammals, as shown by Cuénot and confirmed by Little, homozygous or pure yellow mice are unknown although yellow individuals have long been exploited by fanciers. In other words, all kinds of yellow mice behave as if heterozygous or simplex with respect to yellow color, for when any two yellow mice are bred together they produce a certain percentage of recessives lacking yellow which would not happen if they were pure yellow. Hundreds of yellow in-

[1] W. E. Castle in collaboration with Walter, Mullenix, and Cobb. "Studies of Inheritance in Rabbits." Carnegie Institution Publications, No. 114, 1909.

[2] For further analysis of color inheritance in mammals, consult the masterly series of papers (1917, 1918) by Sewall Wright.

dividuals have been tested but they always produce, in addition to yellow, some non-yellow; that is, black, brown or gray individuals. A proof that the non-yellow individuals are recessive is shown by the fact that when inbred, they produce no yellow offspring; therefore, yellow is dominant in mice, although Castle has shown that it is recessive in rats.

In a Mendelian monohybrid cross, as has been previously pointed out, the expectation is that in the second generation one-fourth of the offspring will be recessives ($DR \times DR$—$DD + 2\ DR + RR$), but when yellow mice are bred together, the percentage of recessives approximates one-third instead of one-fourth. Little, in a total of over 1200 young produced by yellow parents, obtained almost exactly two-thirds yellow. This apparent exception to the Mendelian ratio finds an explanation, however, when it is assumed that *D* (yellow) is a *lethal gene when present in duplex* (*DD*) *form.* The *DD*s drop out entirely which leaves the proportion approximately two *DR*s and one *RR*. This supposition is further supported by the fact that the litters of young from yellow mice are, on an average, only three-fourths as large as normal litters of mice, which is exactly what would be expected if one-fourth (*DD*) of the possible gametic combinations fail to produce offspring. Moreover, evidence of the death *in utero* of the pure yellow mice has been produced by Ibsen and Stiegleder, '17.

Baur cites a similar case of lethal genes in an *aurea*-race of snapdragons (*Antirrhinum*) with yellowish instead of the normal green leaves, which are always heterozygotes since when the factor for "aurea" appears from both parents the homozygous seedling perishes. In his experiments when *aurea*-plants were self-fertilized he actually obtained 543 *aurea* and

286 normal green plants, which is surprisingly near the expected ratio of 2 : 1.

In these instances the lethal factor is a lack of chlorophyll which is not fatal if inherited from a single parent because the deficiency is made good by a gene for chlorophyll from the other parent, but when the lack comes from both parents it produces a seedling unable to survive after the stored food in the seed is used up.

G. H. Shull has demonstrated the existence of two balanced recessive lethal factors in one pair of the fourteen chromosomes in *Œnothera,* one pair producing a lethal effect *in the zygote,* the other pair *destroying the gametes.* This fact explains many of the hitherto confusing ratios obtained in breeding this classical plant.

Only individuals heterozygous with respect to lethal genes survive. When the same kind of a lethal gene comes from both parents, thus rendering the individual homozygous so far as the lethal gene in question is concerned, death results. But whenever non-lethal genes that were previously linked with lethal genes cross over, they may in this way escape from the obliterating influence of their lethal companion genes, and so as a consequence come into phenotypic expression.

The apparently sudden appearance of a new character by this method of "balanced lethals" may easily be mistaken for true mutation, whereas it is simply the release of a suppressed characteristic already present and not the initiation of something new to the germplasm.

That this type of apparent mutation may occur had been repeatedly demonstrated, for example by Bridges and Muller for *Drosophila;* Frost for *Matthiola;* Blakeslee, Belling, and Farnum for *Datura;* and by G. H. Shull for *Œnothera* itself

which has played so important a rôle historically in the whole mutation idea.

Morgan and his associates have demonstrated the existence of over forty different lethal factors in *Drosophila* which when inherited from both parents not only prevent the development of any characters but also doom the individual to death. Only heterozygotes for such lethals which receive the death warrant from one parent alone may escape and hand on this fatal determiner.

"Such lethal factors modify the expected Mendelian ratios and greatly complicate the study of genetics, but they do not destroy its fundamental principles, indeed when properly understood they furnish one of the strongest proofs of the truth of the factorial theory of heredity" (Conklin).

6. Modifying Genes and Selection

The recognition of modifying genes has furnished an explanation for the apparent effectiveness of selection within a pure line *without assuming germinal inconstancy.*

The gene itself, like that producing the hooded pattern of Castle's rats, is *constant* but it is accompanied by a halo of modifying genes likewise constant that have no somatic expression except when the original factor for hooded pattern is present. These modifying genes are simply potential increasers or diminishers of the hooded-pattern gene. In the absence of the pattern gene there is nothing to increase or diminish and consequently there is no way to demonstrate the modifying factors. They are not imaginary things, however, for their separate existence and transmissibility have been demonstrated from many sides. What selection within the progeny of the homozygous cross of hooded rats or bristly flies accomplishes is simply the elimination or addition of

either plus or minus modifying genes, according as the attempt is being made to increase or decrease the hooded pattern of pigmentation or the number of bristles.

The present concept of germplasm is not that of a plastic substance, but of a mosaic made up of a great number of definite and relatively stable units, each fitting perfectly into place.

If this explanation stands the test of further investigation then we are still dealing in heredity with constant dependable units, and it may be said that all genetic roads lead to the Rome of *gene-constancy* on which Mendelism depends.

The evidence increases that the germplasm is relatively constant, while the characters to which it gives expression vary.

The fossil amber ants over two million years old which Wheeler describes as morphologically indistinguishable from living species of today, would indicate that instances of something that bears a strong resemblance to constancy may be found.

Heredity seems to be a complex interweaving of relatively permanent strands, in which the threads vary but little although the pattern may vary much.

However, it is well to remember that Darwin did not revolutionize the concept of evolution until he broke down the idea of constancy of species and that geology did not come into its own until Lyell substituted for immutability the molding hand of incessant change.

Likewise recent advances in modern chemistry have come with the discovery of the Curies that the "immutable elements" are after all capable of transformation, while Einstein has given us the uneasy feeling that all the familiar fixed points of the physical world are shifting.

Perhaps the geneticist will also have to give up eventually

the comfortable dependability of *constant genes,* as new discoveries are made.

Meanwhile constancy of genes is the most fertile working hypothesis at hand, and it still allows at least three ways in which to account for the cumulative modifications wrought by selection in a world of constant units, namely:

(1) By the isolation of pure lines if the stock is hybrid (heterozygous);

(2) By the elimination or addition of modifying genes if the stock is pure (homozygous);

(3) By mutation of the genes.

It should be repeated that change by mutation does not beg the question of constancy of the genes. A mutation is not a changed gene. It is the substitution of an entirely different one.

CHAPTER VIII

BLENDING INHERITANCE

1. Relative Significance of Dominance and Segregation

Of the three fundamental principles which underlie Mendelism, namely, segregation, independent assortment and dominance, the principle of dominance has been found to hold true in a surprising number of cases and in relation to very diverse organisms, notwithstanding the fact that its universal application is by no means assured.

Mendel himself noted certain exceptions to the law of dominance, and his followers have pointed out with increasing emphasis that it is subject to many modifications. It is now understood, indeed, that *segregation, not dominance,* is the most essential factor in the Mendelian scheme. The difficulties in demonstrating segregation have been largely due to the assumption that visible differences are unit characters represented by single determiners.

2. Imperfect Dominance

It frequently occurs that dominance is so imperfect that a heterozygous, or simplex, dominant may be distinguished at once by simple inspection from a homozygous, or duplex, dominant, whereas the test of crossing with a recessive is necessary whenever dominance is complete, as has been previously explained. The single dose of the determiner in such a case has plainly, then, less phenotypic effect than a double dose.

There are many instances of imperfect dominance among flowering plants. Correns' red and white four-o'clocks with pink offspring (p. 105) is a case in hand.

A classic illustration of imperfect dominance among animals is the "blue Andalusian fowl," the hereditary behavior of which is illustrated below (Fig. 35). It will be seen that when two blue Andalusian fowls, characterized by a mottled plumage, are bred together, they produce three kinds of offspring in the Mendelian ratio of 1 : 2 : 1. Twenty-five per cent

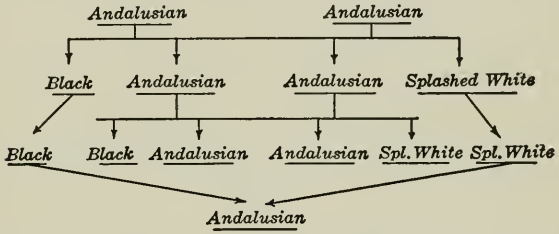

Fig. 35.—The heredity of the blue Andalusian fowl, an illustration of "imperfect dominance."

are clear black, 50 per cent are blue Andalusian, and 25 per cent are white splashed with black. Both the black and the splashed-white fowls from this cross prove, upon further breeding, to be homozygous, while the blue Andalusian itself is heterozygous and can, therefore, never be made to breed entirely true. In order to produce 100 per cent of blue Andalusian chicks, it is only necessary to cross a splashed-white with a black Andalusian.

There is nothing in this case to indicate whether the black or the splashed-white should be regarded as the homozygous dominant, since dominance is imperfect. In either case the heterozygous blue Andalusian is at once evident in the first filial generation without further crossing.

A similar case of imperfect dominance is furnished by the roan color of cattle which results when red and white are crossed. If two roans are mated, they produce red, roan, and white offspring in the proportion of 1 : 2 : 1, thus showing that roan is a heterozygous character in which the dominance of red is imperfect.

Even in cases of apparently perfect dominance it is sometimes possible by close inspection to detect differences between a pure dominant (*DD*), Figure 17, and a heterozygous dominant (*DR*) when a superficial examination is not sufficient to distinguish them.

Morgan cites a *Drosophila* cross between "ebony" and "sooty" wings in which the F_2 generation ranges from ebony to sooty in an inseparable transition but it proves, nevertheless, to be of three classes in the proportion of 1 : 2 : 1, as further breeding tests show.

3. Delayed Dominance

A character which is really dominant is sometimes so late in manifesting itself in the individual growth of the offspring that it may properly be termed a *delayed dominant.*

Dark-haired individuals often do not acquire their definitive hair color until adult life, and it is common knowledge that the eyes of an infant for a considerable period provoke no little speculation among adoring relatives as to "whose eyes" they are.

According to Davenport, when a white Leghorn fowl is crossed with a black Leghorn, white being dominant in this case, chicks are produced that are *white with black flecks in their plumage.* These black flecks, however, disappear at the time of the first molt. The complete dominance of white is, therefore, simply delayed.

4. Reversed Dominance

In certain instances there seems to be a reversal of dominance, as may be illustrated by Lang's results with snails (*Helix*). He has proven in his experiments that red snails are generally dominant over yellow snails, although in certain cases there is apparently an exception to the rule, for snails with yellow shells dominate those with red shells.

Davenport has shown, too, that although extra toes are usually dominant over the normal number in poultry, yet, in something like 20 per cent of the cases, the normal number is dominant.

It sometimes occurs that a character which is dominant in one species may be recessive in another. Horns are dominant in sheep, but recessive in cattle. White color is recessive in rodents and sheep, but dominant in most poultry and in pigs.

Yellow color is dominant in mice but recessive in rats. Notched margin in leaves is a dominant characteristic in nettles but recessive in the celandine. Baldness is dominant in the human male and recessive in the female.

5. Conditioned Dominance

Morgan describes a kind of *Drosophila* possessing a gene for abnormally banded abdomen which does not come to somatic expression unless the flies are supplied with fresh food and a proper amount of moisture. When the food becomes dried up and there is a minimum of moisture, the banding on the abdomen disappears. Here is a type of dominance conditioned upon certain environmental factors.

Blakeslee reports *Daturas* that show a purple stem when grown out-of-doors but green if kept in the greenhouse, and Baur found that *Primula sinensis rubra,* kept at a temperature

of 30° to 35° C. for a week before blooming, will develop white flowers, but at lower and more normal temperatures of from 15° to 20° C. will prove true to its name and produce red flowers. Red is dominant over white in *Primula* but its appearance is conditioned by certain limits of temperature.

6. Negative Dominance

A negative character may be the dominant one in a pair of allelomorphs. For example, the bob-tail of the Manx cat is dominant over the ordinary long tail of the cat; the reduced number of three digits in guinea pigs is dominant over four digits; the polled condition is dominant over horns in cattle; the rumpless fowl is dominant over the fowl with a rump, and brachydactyly in man, that is, fingers or toes with only two joints each, is dominant over the three-jointed arrangement.

"Dominance says nothing as to the positivity of any factor, but it indicates only that a factor (or its absence) is able to realize the character or reaction in question *even in case of heterozygosis*. Recessivity means only that homozygosis (+ or —) is necessary for the realization of the reactions in question" (Johannsen).

7. Epistasis

When two factors that are not allelomorphic to each other act upon the same character and one forestalls the expression of the other, *epistasis* occurs, a condition that resembles dominance between the genes of a single allelomorphic pair but is something quite different. In dominance one factor covers up or conceals its allelomorphic mate, so far as somatic expression goes. In epistasis, on the other hand, a factor from one pair of allelomorphs interferes with the action of other allelomorphic factors that exercise an influence on the same char-

acter. Thus in hair-form there is an ascending relationship between the genes for straight, wavy, curly, and kinky condition such that each kind in the series as indicated is dominant to all neighboring kinds on its left and recessive to all on its right. Curly hair, for example, is dominant to wavy but when matched with kinky hair is recessive and becomes obliterated.

8. Potency

Davenport seeks to explain modifications in typical dominance as variations in the *potency* of determiners. He defines potency as follows: "The potency of a character may be defined as the capacity of its germinal determiner to complete its entire ontogeny."

That is, if the potency of a determiner, for some reason, is insufficient, there may be either an incomplete or delayed manifestation of the character in question, or it may fail entirely to develop.

The variations of potency may be grouped into three general categories according to the degree of their manifestation, namely, total potency, partial potency, and failure of potency.

A further word of explanation for each of these three kinds of potency seems desirable at this point.

A. TOTAL POTENCY

This is typical of complete Mendelian dominance in which even the heterozygotes produced by a simplex dose of a character are indistinguishable phenotypically, that is, by inspection, from the homozygotes produced by a duplex dose of the same character. It is as if a single bottle of black ink poured into a jar of water was just as effective as *two* bottles of ink, in forming an opaque fluid.

Even in some cases of apparently complete dominance, refined methods of examination or analysis may make it possible to distinguish the duplex from the simplex condition without recourse to breeding. Darbishire has shown, in the case of Mendel's smooth and wrinkled peas, that the two kinds of smooth progeny from the F_1 hybrid upon microscopic examination show a difference in their starch grains, indicating at once which is homozygous and which is heterozygous. Moreover, in the power of absorption, hybrid smooth peas (*DR*) are intermediate between their pure dominant smooth (*DD*) and pure recessive wrinkled (*RR*) parents.

Blakeslee has demonstrated a chemical method of distinguishing unseen genetic differences in the apparently similar flowers of the black-eyed Susan (*Rudbeckia hirta*). When placed in a solution of KOH, the yellow cones of one kind turn a purplish-black, while the other kind turns red.

B. PARTIAL POTENCY

Partial potency covers all cases of *incomplete dominance,* such as those of the four-o'clock (*Mirabilis*) and blue Andalusian fowls, where a simplex dose of a determiner does not produce the same visible effect as a double dose.

The dominant prickly jimson weed (*Datura*), when crossed with a recessive glabrous variety of the same plant, produces cross-breds in the first generation which show only a few prickles (Bateson) (Baur), following the law of partial potency.

Banded and uniformly colored snails also, when crossed together, produce snails with shells showing only a pale banding (Lang).

Numerous further instances of incomplete dominance could be cited.

C. FAILURE OF POTENCY

If for any reason a determiner fails to accomplish its possibilities in whole or in part, then the character in question may never become evident, and the result, so far as appearances go, is the same as if it was a recessive lacking the determiner entirely.

That the failure of potency is not identical with the absence of a determiner can usually be demonstrated by further breeding, because dominants failing in potency, which are either of the formula *DD* or *DR,* may, if bred *inter se,* give a various progeny among which the dominant character *D* is likely to become manifest again, while recessives of the formula *RR,* on the contrary, will invariably give offspring which all agree in the entire absence of the character in question.

Davenport cites an extreme case of failure of potency in one of two rumpless cocks from the same blood. The character of rumplessness is due to an *inhibitor* of tail development. That these two cocks both possessed this character was demonstrated by the entire absence of any tail in either case. The inhibiting determiner for tail growth was so weak in cock No. 117 as to have no inhibiting value. To quote Davenport's exact words: "In the heterozygote the development of the tail is not interfered with at all, and even in extracted dominants it interfered little with tail development, so that it makes itself felt only in the reduced size of the uropygium and in-bent or shortened back. But in No. 116 the inhibiting determiner is strong. It develops fully in about 47 per cent of all the heterozygotes and in extracted dominants may produce a family in *all* of which the tail's development is inhibited."

Here were two birds of the same blood, phenotypically alike and presumably genotypically alike, which because of an individual difference in the potency of the determiner for rumplessness produced quite different results in their offspring although bred to precisely the same array of hens.

9. Blending Inheritance

In the instances of imperfect dominance given above, where the progeny of unlike parents present an intermediate condition, it is found that, upon cross-breeding these offspring, segregation into the grandparental types occurs just as truly as in instances of complete dominance.

In poultry, for example, when Cochins, which are "booted," and Leghorns, which are clean-shanked, are crossed, booting of an intermediate grade of four results, on a scale in which ten represents complete booting, and zero, no booting or clean shank (Davenport). The character of booting and its alternative absence, however, segregate out in true Mendelian fashion when these hybrids are subsequently crossed together. It is evident that dominance plays only a secondary rôle in such cases, and that the all-important factor is segregation.

Are there, then, any cases where true fusion of hereditary parental traits occurs, in other words, where *segregation in the second filial generation does not appear?* Does the "melting-pot of cross-breeding" ever "melt" the characters thrown into it?

Early hybridizers, regarding the *individual as the unit,* naturally gave credence to the belief that diverse parents generally produce intermediate offspring, particularly with quantitative characters such as size and weight, and that this intermediate condition continues without any segregation at all in the form of "blending inheritance." Within the last two

decades, however, apparent cases of blending inheritance have been thrown out of court one after the other by the Mendelians. Bateson, in an inaugural address at Cambridge University in 1908, stated that what was once believed to be the rule has now become the exception. He goes on to say: "One clear exception I may mention. Castle finds that in a cross between the long-eared lop rabbit and a short-eared breed, ears of intermediate length are produced; and that these intermediates breed approximately true."

10. The Case of Rabbit Ears

Let us examine this "one clear exception" a little more closely.

As a typical example of blending inheritance in rabbit ears the following case may be cited:

A female Belgian hare with an ear-length of 118 mm. was crossed with a male lop-eared rabbit with an ear-length of 210 mm., the average of these ear-lengths being 164 mm. Five offspring from this pair had ear-lengths, when adult, approximating this average as follows: 170, 170, 166, 156, 170, of which two were females and three were males. When from this litter one of the females measuring 170 mm. in ear-length was subsequently crossed with her brother having an ear-length of 166 mm.,. two litters were produced in which the individuals when adult attained ear-lengths of 170, 166, 168, 160, 172, and 168 mm. These results are represented diagrammatically in Figure 36.

This illustration is typical of many other breeding experiments made by the same investigators [1] upon the ear-length

[1] Castle, in collaboration with Walter, Mullenix and Cobb. "Studies of Inheritance in Rabbits." Carnegie Institution Publications, Washington, No. 114, 1909.

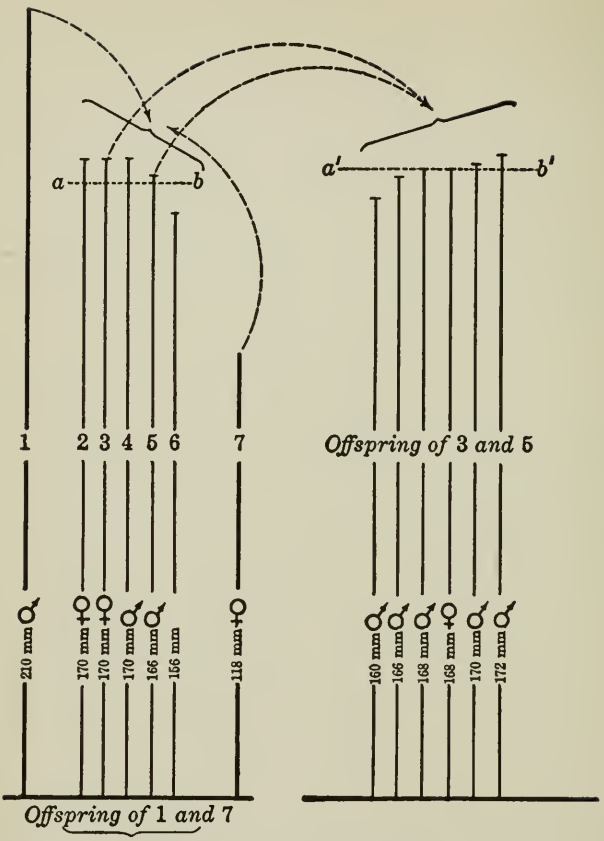

FIG. 36.—A case of three generations of ear-length in rabbits. *a-b*, average ear-length of the first filial generation (F_1). *a'-b'*, average ear-length of the F_2 generation derived from 1 and 7. Data from Castle, in collaboration with Walter, Mullenix and Cobb.

of rabbits which included 70 different litters of rabbits containing 341 individuals. In none of these experiments could the blend in the second filial generation be called perfect, but it may at least be said that evidence of segregation, that is, a

return to one or the other of the parental types, was much less apparent than evidence of blending.

Furthermore, crosses were made in which lop ears of various fractional lengths were obtained as desired, including ⅛, ¼, ⅜, ½, ⅝, ¾, and ⅞ lengths. Not one of these fractional lengths apparently segregated in subsequent generations after the Mendelian fashion, but all bred approximately true.

Moreover, ears of ½ lop length, for instance, were obtained in three ways: first, by crossing full-length lops with short-eared rabbits as indicated in the first cross of the case cited above; second, by crossing ½ lop lengths together, demonstrated by the second cross in the illustrative case given, and third, by mating ¼ and ¾ lop lengths. Theoretically, ⅛ and ⅞ as well as ⅜ and ⅝ lop lengths would also produce ½ lop lengths, for in all of the crosses that were made the length of the ear behaved in a blending fashion.

These results were based, not upon a single measurement of each specimen, which might be open to considerable error, but upon daily measurements from the time the rabbits were two weeks old until their ears ceased to grow at about twenty weeks. The growth curves drawn from these daily measurements showed continually an intermediate or blending condition in progeny derived from diverse parents.

A Mendelian explanation of this apparently exceptional case of blending inheritance has been suggested by Lang, based upon the result of Nilsson-Ehle's discoveries while breeding wheats at the Agricultural Experiment Station of Svalöf in Sweden.

11. The Nilsson-Ehle Discovery

In breeding together different strains of wheat Nilsson-Ehle found in 1907 that a certain wheat with brown chaff

crossed with a white-chaffed strain yielded only brown-chaffed wheat in the first generation. These heterozygous or hybrid brown-chaffed wheats when crossed with each other produced, not the expected proportion of three brown to one white, but *fifteen brown to one white.* This was not explainable as the chance result of a single cross, but was the conclusion drawn from several different crosses, all of the same strains, that yielded a total progeny of 1410 brown-chaffed to 94 white-chaffed plants, which happens to be exactly the proportion of fifteen to one.

In other experiments it was discovered that although dominant red-kerneled strains of wheat crossed with white-kerneled varieties usually gave the three-to-one proportion upon segregation in the second filial generation, yet *one particular strain* of red-kerneled Swedish wheat in the second generation gave approximately sixty-three red to one white-kerneled strain.

The explanation of these two unexpected results is this. In the case of brown-chaffed wheat there are two independent duplicate determiners for the character of brown color, and these simply follow the Mendelian laws for a dihybrid, while in the case of the red-kerneled wheat there are three independent duplicate determiners for the character of red color, each of which is able to give red color to the wheat. Taken together, these three red color determiners behave *cumulatively,* while following the law of a trihybrid.

For example, if a brown-chaffed wheat with the formula BB', in which B and B' each represent a brown-chaffed factor, is crossed with a white-chaffed wheat of the formula bb', in which b and b' each represent the absence of B and B' respectively, then all the progeny of this cross will be brown-chaffed, having the zygotic formula $BB'bb'$. When upon

maturation the gametes form out of the germ-cells from such hybrids, the following four combinations are possible, and no others: *BB′*, *Bb′*, *bB′*, *bb′*. These represent, therefore, the possible gametes present in each sex of the first filial generation, and upon intercrossing they may combine into sixteen possible zygotes to form the second filial generation, as shown in Figure 37.

	BB′	*Bb′*	*bB′*	*bb′*
BB′	*BB′* *BB′* ④	*Bb′* *BB′* ③	*bB′* *BB′* ③	*bb′* *BB′* ②
Bb′	*BB′* *Bb′* ③	*Bb′* *Bb′* ②	*bB′* *Bb′* ②	*bb′* *Bb′* ①
bB′	*BB′* *bB′* ③	*Bb′* *bB′* ②	*bB′* *bB′* ②	*bb′* *bB′* ①
bb′	*BB′* *bb′* ②	*Bb′* *bb′* ①	*bB′* *bb′* ①	*bb′* *bb′* ⓪

FIG. 37.—Diagram of the possible combinations in the F_2 generation of brown-chaffed wheat according to experiments of Nilsson-Ehle. *B* and *B′* are cumulative factors for the brown-chaff character; *b* and *b′* denote the absence of *B* and *B′* respectively.

The numbers in the squares in Figure 37 indicate how many times a brown determiner is present in each zygote. It will be seen that only one out of the sixteen possibilities lacks a brown-chaffed factor, and this one will consequently produce only white chaff, while the remaining fifteen possibilities, each of which has at least a single determiner for brown, will consequently all yield brown chaff.

The brown-chaffed factor, moreover, is present in varying doses among these fifteen possibilities, as indicated by the numbers in the squares. It is evident, therefore, that several shades of brown will be represented, depending upon the number of doses of the brown determiner in each instance.

Figure 38 shows how these different shades of brown arrange themselves in the manner of a frequency curve of fluctuating variation with the greatest number in the halfway class and the least numbers at the two extremes. In this instance six out of sixteen individuals of the second generation

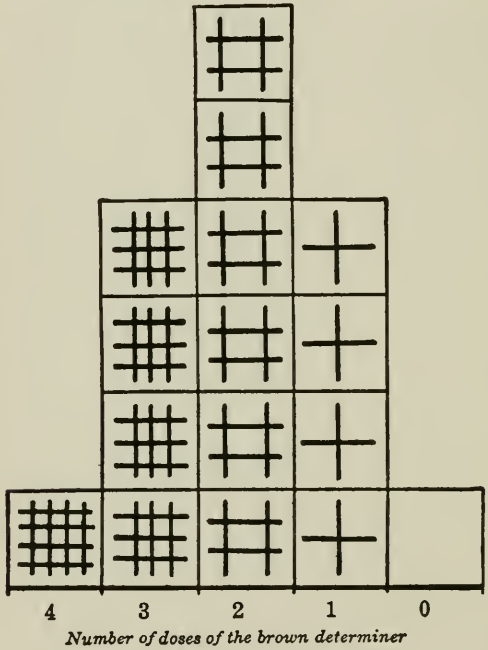

FIG. 38.—The distribution of the sixteen possibilities resulting when two similar determiners (brown-chaff) act together as a dihybrid.

theoretically present a perfect "blend" between the original brown- and white-chaffed grandparents, although complete segregation has actually occurred.

The same explanation holds true as displayed in Figure 39 for the trihybrid case of red- and white-kerneled wheats in which only one white-kerneled to sixty-three red-

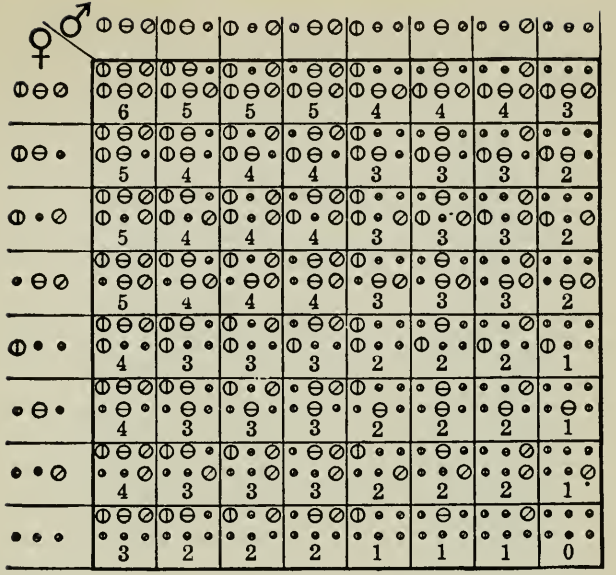

Fig. 39.—Diagram to illustrate Nilsson-Ehle's case of trihybrid red wheat. The large screw-heads each represent a single determiner for the red character. The small screw-heads symbolize the absence of the red character, or white. The number in each square indicates how many doses of the "red" determiner is present. For further explanation see text.

kerneled individuals appear in the second filial generation. The number of red determiners in each zygote is indicated by the figure at the bottom of each square. The large screw-head symbols with vertical, horizontal and diagonal slots each represent an independent determiner for red kernel, while the small screw-heads symbolize the corresponding absence of each of these determiners,

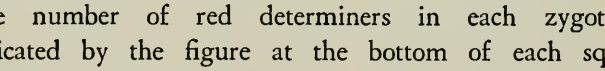

Fig. 40.—The result of crossing white wheat with trihybrid red wheat.

or white kernel. When the pure strain of red-kerneled wheat is crossed with a pure strain of white-kerneled wheat, the first generation is all a heterozygous red of a somewhat lighter shade than the original pure red strain, as shown diagrammatically in Figure 40.

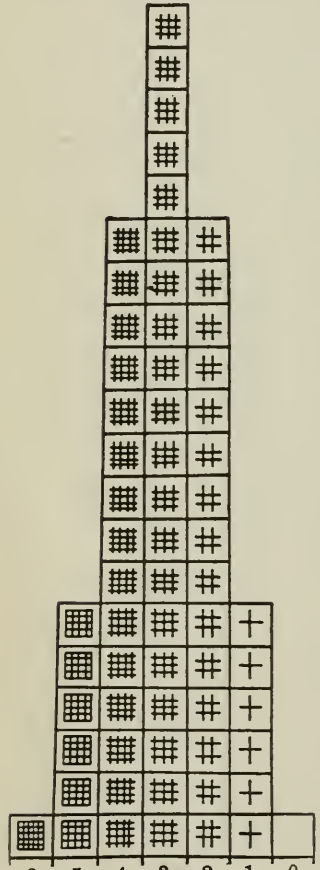

Fig. 41.—The distribution of the sixty-four possibilities in the F_2 generation when three similar determiners act together as a trihybrid.

When plants of this heterozygous sort are crossed together, they yield plants producing red-kerneled and white-kerneled wheats in the proportion of sixty-three to one. The sixty-three kinds of red wheats are of varying degrees of redness and may be classified after the manner of fluctuating variations with the greatest number (20) of kinds at the intermediate degree between pure red and pure white. (Figure 41.)

In order to test whether the sixty-four kinds of wheats produced in the second filial generation, as theoretically displayed in Figure 39, really contain separable, though indistinguishable, determiners for red kernel, Nilsson-Ehle produced families of the third filial generation by self-crossing plants of the second generation. It was to be expected that, if these hybrid wheats of

the second generation carried one, two, three, or more determiners for a red kernel as the theoretical tables in Figures 39 and 41 demand, their progeny would be distributed with reference to the number of red- and white-kerneled individuals in the following ratios:

3 red to 1 white when 1 heterozygous determiner for red is present.
15 red to 1 white when 2
63 red to 1 white when 3
All red to no white when 4 or more } heterozygous determiners for red are present.

Among seventy-eight sample families of the third generation inbred to test this theoretical conclusion, the actual results were:

8 families giving the ratio of 3 red to 1 white.
15 families giving the ratio of 15 red to 1 white.
5 families giving the ratio of 63 red to 1 white.
50 families giving the ratio of all red to no white.

It has been actually demonstrated, therefore, in the case of this particular strain of wheat: (1) that the factors producing red kernels are several in number; (2) that they act independently of each other in heredity; (3) that these several independent duplicate factors segregate; and (4) that any one red factor acting alone produces a "red" result.

The Nilsson-Ehle principle of duplicate determiners has been confirmed in America by East in a masterly series of breeding experiments upon maize.

In connection with the Nilsson-Ehle principle, it will be seen that the possible number of intergrades between the two extremes increases rapidly as the number of duplicate determiners increases. Thus with six duplicate determiners for the same character present, the ratio of possible dominants to recessives in the second filial generation would be 4095 to 1. The reappearance of this single recessive among 4095 domi-

nants would be extremely unlikely, and it might easily be mistaken for a mutation or a freak. Apparent blends of all intermediate degrees, however, would be sure to appear. Yet these are not blends in the "melting-pot" sense at all, but strictly cases of Mendelian dominance and segregation.

12. The Application of the Nilsson-Ehle Explanation to the Case of Rabbit Ear-Length

The so-called blending rabbit ears, along with other similar cases, can now be made to fall into line, as pointed out by East and by Lang, with the Mendelian law of segregation.

If we assume that the long ear of the lop rabbit has only three independent but equal determiners for *excess length,* the case becomes one of Mendelian trihybridism with duplicate factors, which works out like Nilsson-Ehle's red-kerneled wheat in the following manner:

In general the average for full lop ear-length may be placed at 220 mm. and for the ordinary short-eared rabbit[1] at 100 mm. The difference, or *the excess length of the lop ear,* is 120 mm., which, according to the trihybrid formula, corresponds to the six doses of the character symbolized in the upper left-hand square in Figure 39 by six large screw-heads, three coming from each parent respectively. If all of these independent determiners are equal as regards excess ear-length, each factor would represent an excess of 20 mm. above the normal ear-length found in short-eared rabbits, that is,

$$\frac{220 \text{ mm.} - 100 \text{ mm.}}{6} = 20 \text{ mm.}$$

When according to this computation a lop (20 mm. $\times$ 6 $+$

[1] Not the Belgian hare, as cited in the illustration given in Figure 36. The Belgian hare has typically a somewhat longer ear than the ordinary short-eared rabbit.

100 mm. = 220 mm.) and a pure short-eared rabbit (20 mm. × 0 + 100 mm. = 100 mm.) are crossed, if imperfect dominance occurs, which is a very common phenomenon, it is true that the offspring might present a "blended" appearance. If now these cross-breds of the first generation prove to be trihybrids with respect to excess ear-length, there would be sixty-four possibilities in their progeny segregating out just as in the red-kerneled wheat.

These possibilities would be arranged in the following frequencies:

Number of Excess Ear-length Determiners	Number of Cases Occurring Out of 64	Total Length in Millimeters of Ears Resulting
6	1	220
5	6	200
4	15	180
3	20	160
2	15	140
1	6	120
0	1	100

Since the average litter among rabbits is about five, the chances that any one of these five rabbits will breed true to their hybrid parents and form a perfect blend between their grandparents is 20 out of 64, while the chance of any given one being like one or the other grandparent is only one out of 64.

It should be noted further that 50 out of 64, that is, 77 per cent of these hybrids of the second filial generation, would have an ear-length between 140 and 180, thus approximating a "blend" closely enough to be so classified upon a casual inspection.

If it should be found, moreover, that excessive ear-length in rabbits is due to more than three duplicate determiners, the

possibilities of getting anything but an apparent blend would be much decreased.

13. Human Skin Color

Finally, in man the skin color of mulattoes, which are hybrids between blacks and whites, has often been mentioned as a case of blending inheritance, since mulattoes are commonly supposed to produce mulattoes when they mate together or a blending degree of color when they mate with some one whose shade of color is unlike their own.

This matter has been carefully and extensively studied by

	AB	*Ab*	*aB*	*ab*
AB	*AB* *AB* 70	*Ab* *AB* 55	*aB* *AB* 53	*ab* *AB* 38
Ab	*AB* *Ab* 55	*Ab* *Ab* 40	*aB* *Ab* 38	*ab* *Ab* 23
aB	*AB* *aB* 53	*Ab* *aB* 38	*aB* *aB* 36	*ab* *aB* 21
ab	*AB* *ab* 38	*Ab* *ab* 23	*aB* *ab* 21	*ab* *ab* 6

Fig. 42.—Checkerboard to show the different expected shades of black color in the possible offspring of two mulattoes. A = 19; B = 16; a = 2; b = 1 per cent of black pigment. Data from Davenport and Danielson.

Davenport and Danielson [1] who came to the conclusion that the pure-blooded negro of the West Coast of Africa possesses two pairs of duplicate genes for black pigmentation (*AABB*) which, though separately heritable, are cumulative in effect. The corresponding formula for black pigmentation in a normal white is *aabb*. When black (*AABB*) and white (*aabb*) are crossed, the formula for the mulatto will be *AaBb* in which half the total amount of black pigment of both parents is present.

The result of crossing two mulattoes is shown by the checkerboard diagram in Fig. 42.

The figures in the corners of the squares indicate the total amount of black pigment in each case upon the supposition that $A = 19$, $B = 16$, $a = 2$ and $b = 1$, these values being

A Classification of Hybrid Skin Colors on the Basis of the Factor Hypothesis

Genes	Gametic Formula	Color	Relative Frequency	Range of Per cent of Pigment in Offspring	Popular Names (Jamaica)
All absent . .	aabb	White	1:16	0–11	Pass-for-white Mustifino Mustifee Octaroon
One present .	Aabb aaBb	Light	4:16	12–25	Quadroon
Two present .	AAbb AaBb aaBB	Medium	6:16	26–40	Mulatto
Three present .	AABb AaBB	Dark	4:16	41–55	Mangro Sambo
All four present	AABB	Black	1:16	56–78	Negro

[1] "Heredity of Skin Color in Negro and White Crosses." Pub. No. 188 of the Carnegie Inst. of Washington.

determined by the color-top method described by Davenport and Danielson.

In the table on page 185 there is a classification of these possibilities according to the amount of black pigment present, and in Figure 43, a graphic representation of the numerical

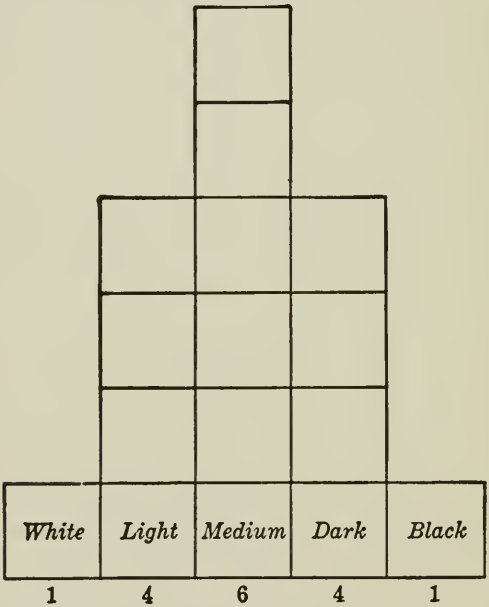

Fig. 43.—Diagram to show the expectation of color and its frequency in the cross between two mulattoes.

chances for skin color in spite of segregation when two mulattoes mate.

The case thus is similar to that of Nilsson-Ehle's brown-chaffed wheat already described, so that the possible range of offspring of a mulatto pair is all the way from black to white. Theoretically, any one of five degrees of pigmentation, including the extremes of black and white, may be expected. The

chances which any one of these five degrees of color has of reappearing in a child of mulatto parents is indicated in Fig. 43. It is evident that there is more likelihood, in point of fact six chances out of sixteen, that a child from mulatto parents will be mulatto rather than anything else, and this expectation ordinarily agrees with the realization, but there are four chances out of sixteen that it will be either slightly darker or lighter than its parents and one chance out of sixteen that it will be as dark or as light as its black or white grandparents.

Davenport and Danielson show several illuminating photographs of large families of children from mulatto parents in which a manifest inequality of color shade among the different children is apparent as would be expected according to this explanation.

Blending inheritance, then, is probably nothing more than Mendelian alternative inheritance in which two or more similar genes, duplicate or cumulative, are concerned. Just as a curve may be conceived to be a series of very minute straight lines, so "blends" may be regarded as a series of Mendelian segregations. Granting this assumption to be true, one explanation instead of two or three, consequently, is sufficient to dispose of an array of apparently diverse phenomena.

"We may therefore conclude," says Conklin, "that the Mendelian law of heredity, especially as regards segregation of inheritance factors, is of universal occurrence—that there is no other type of inheritance."

CHAPTER IX

OLD TYPES AND NEW

1. The Distinction between Reversion and Atavism

There are two ways in which types of animals or plants that are different from the present ones may be conceived to arise, namely, by the reappearance of old types and by the formation of new ones. In the reappearance of old types a distinction may be drawn between reversion and what has been termed atavism.

Atavism, or "grandparentism," may be defined as skipping a generation with the result that a particular character in the offspring is unlike the corresponding character in either parent, but instead, resembles the character in one of the grandparents.

In *reversion,* on the contrary, a character reappears which has not been manifest perhaps for many generations, although it was actually present in some remote ancestor. J. Arthur Thomson's definition of reversion is: "All cases where through inheritance there reappears in an individual some character which was not expressed in his immediate lineage, but which had occurred in a remoter, but not hypothetical, ancestor."

This distinction between atavism and reversion becomes clearer by illustration.

If heterozygous brown-eyed individuals mate, there is one possibility in four that their offspring will have blue eyes

unlike their own, but like the two blue-eyed grandparents. Such a blue-eyed child would be an instance of atavism. The explanation of this apparently inconsistent hereditary behavior

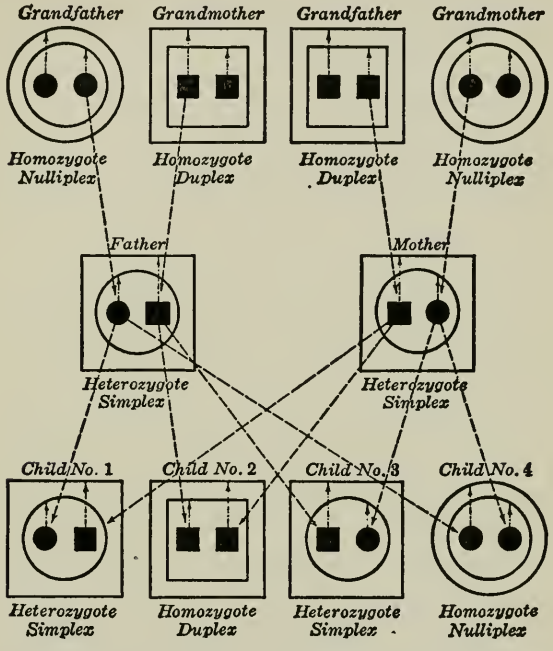

FIG. 44.—Three generations of a Mendelian monohybrid. The outlines represent the somatoplasms with the phenotypic character on the outside. The black symbols inclosed within the somatoplasm stand for the germplasm in the form of gametes. The short dotted arrows indicate the relation between germplasm and somatoplasm. The long dotted arrows indicate possible recombinations of germplasms.

is perfectly simple in the light of the Mendelian ratios, as shown diagrammatically in Figure 44, in which the circles represent the blue-eyed and the squares the brown-eyed character.

This figure also illustrates what typically occurs in the

formation of Mendelian monohybrids of the first and second filial generations. The squares are symbols for the *dominant* characters, while the circles are symbols for the *recessive* characters. When the two are superimposed, the circle recedes from view. The large outside figures in outline indicate the *somatoplasm,* therefore the *phenotype.* The small inclosed solid black figures indicate the *germplasm,* therefore the *genotype.* The short dotted arrows indicate what it is that determines the somatoplasm in each case, while the long dotted arrows show what possible recombinations of germplasms can be made. Child No. 4 is an "extracted recessive" derived from dominant parents, but with one recessive grandparent on each side. It is a case of "atavism," or taking after the grandparent. It should be noticed that atavism can occur only by alternative inheritance.

To quote Davenport: "In the majority of cases atavism is a simple reappearance in one-fourth of the offspring of the absence of a character due to the simplex nature of the character in both parents."

An illustration of *reversion* would be the reappearance of the ancestral jungle-fowl pattern in domestic poultry or of the slaty blue color of the ancestral rock-pigeon among buff and white domestic pigeons, for ancestral characters in this type of hereditary behavior, as said before, reappear only after a lapse of many generations.

2. False Reversion

"Around the term 'reversion,'" Bateson observes, "a singular set of false ideas have gathered themselves." In proof of this statement there may be cited at least five categories of apparent reversion which properly ought not to be classed as true reversion.

A. ARRESTED DEVELOPMENT

Feeble-mindedness is not reversion to ancestral forms of less intelligence, but an instance of *arrested development* when, for some reason, the individual fails to accomplish his normal cycle of development.

Likewise harelip in man is not a case of reversion to rabbit-like ancestors in which harelip is the normal condition, but it is ordinarily due to an arrest or failure of certain embryonic processes essential to the development of the usual form of human lip.

B. VESTIGIAL STRUCTURES

These are the vanishing remains of characters that were formerly of significance. They do not represent something latent that is now *re*appearing, for they have never yet *dis*-appeared phylogenetically, and consequently they cannot be regarded as true reversions.

The muscles under the scalp which enable those persons possessing them to wiggle the ears; the palatine ridges in the roof of the mouth of many babies and some adults which resemble the ridges in the roof of a cat's mouth; the vermiform appendix, a necessary part of the digestive apparatus of many animals but so often fraught with evil consequences to man; these and scores of similar characters, that, taken together, make man in the eyes of the comparative anatomist a veritable old curiosity shop of ancestral relics, are the last traces of characters which formerly had a significance in some of man's forbears. Having lost their usefulness, these structures still hang on to the anatomical household as pensioners. They have not been recalled from the past, but have always been with us, although of diminishing importance. In no sense, therefore, can they be called reversions.

C. ACQUIRED CHARACTERS RESEMBLING ANCESTRAL ONES

Sometimes the drunken descendant of a drunken great-grandparent has acquired this characteristic through his own initiative quite aside from any ancestral contribution to his germplasm. This is not reversion, but independent secondary acquisition resembling the ancestral condition.

Again, tame animals that run wild acquire habits resembling those of their wild ancestor, but this is not necessarily reversion. It is the natural response of feral animals to the conditions of wild life.

D. CONVERGENT VARIATION

The European hedgehog, *Erinaceus,* an insectivore, the American porcupine, *Erithizon,* a rodent, and the Australian spiny anteater, *Echidna,* a monotreme, are all mammals which have developed in a similar manner the very peculiar device of integumental spines. There is no reason, however, for regarding this character as due to descent from a common spiny ancestor. It is not reversion to an ancestral type, but rather a case of convergent variation. Similarity does not always indicate genetic continuity.

In the case of birds albinism, melanism and flavism are modifications of ordinary pigmentation which appear irregularly among many different species as pathological "sports," but no one of these conditions can be regarded as reversions to ancestral white, black, or yellow types.

E. REGRESSION

Galton's "law of regression" refers to the widespread phenomenon already explained of a constant swinging back to mediocrity which the breeder must oppose with continual selection in order to maintain the standard of any particular

strain. We have seen that within a "pure line," regression is usually complete and that in populations made up of a mixture of pure lines it is a factor that must invariably be considered. Regression, however, has to do with fluctuating variations and does not bring about a permanent change of type. It should, therefore, not be confused with reversion.

3. Explanation of Reversion

Darwin, who did not always differentiate between reversion and atavism, suggested that reversion was due sometimes to the action of a more natural environment, as in the case of animals set free after having been in captivity, and sometimes to hybridization, since there seems to be a general tendency of hybridized organisms to "revert" to ancestral types.

It is now known that reversion, like atavism, is simply a case of latent characters becoming apparent according to the Mendelian principle of segregation. To quote Davenport: "There is nothing more mysterious about reversion, from the modern standpoint, than about forming a word from the proper combination of letters."

4. The Art and Science of Breeding

The *art* of breeding animals and plants has been practiced from very early times, while the *science* of maintaining old types and initiating new ones is of comparatively recent origin.

Some of the methods that have been employed with varying degrees of success are:

A. Mass selection;
B. Pedigree breeding;
C. Inbreeding;
D. Hybridization;
E. Genotypic selection.

A. MASS SELECTION

The natural thing to do in the maintenance or improvement of cultivated plants and domestic animals is to select seeds from the best-looking plants and to breed together from the flock or herd those animals which appear most desirable. This has been the method from the beginning and there is a reason for the considerable degree of success that has followed this obvious mode of procedure. The method, however, has its limitations because it is *entirely phenotypic* and the breeder is sure to find with Dryden that "all as they say that glitters is not gold."

Two methods of mass selection, as applied to plants, may be mentioned that differ in the extent to which the environment is recognized as a contributing factor.

a. The Method of Hallet

The English wheat-grower Hallet formulated this method in 1869 and it has been in common use for a long time. It consists in placing the organisms to be bred in the very best possible environment and then choosing those individuals making the best showing as the stock from which to breed further, a procedure based upon the deep-seated belief that acquired characters are inherited.

For example, in a field of wheat, plants near the edge of the field which, from lack of crowding or by reason of proximity to an extra local supply of fertilizer or any other favorable environmental factor, make a more vigorous growth than their neighbors, are selected in the hope that the gains made by them will be maintained in their offspring.

We have seen that it is very questionable whether acquired characters due to environmental conditions play any rôle

whatever in heredity. The phenotypic character does not always indicate what the germplasm will subsequently do, and when the true genotypic constitution of the germplasm is still further masked by the temporary fluctuations caused by a modified environment it is increasingly difficult to select wisely from the display of variants those which will produce the best ancestors for the future stock.

That this common procedure of selecting the best-appearing animals in the flock and the biggest ear of corn in the bin has met with a large degree of success in the past is due entirely to the fact that in many instances the phenotypic character is an actual expression of the genotypic constitution. This is not always the case, however, and we cannot now fail to see that the method is blind and full of error. An Arab proverb says: "Avoid the rank plant that grows on a dunghill." Its successes are due to the indirect results of chance rather than to a direct control of the factors of heredity.

Large seeds usually have more stored nutriment and get a better start in life, so also do large eggs, having more yolk.

b. The Method of Rimpau

Contrasted with the method of Hallet of augmenting acquired characters and then selecting from them the best display, is the method of Rimpau, who experimented for two decades with various grains and, finally, among other results, produced the famous Schlandstedt barley.

Rimpau's method is to sow grain under ordinary conditions with a minimum rather than a maximum amount of fertilizer and then to select individuals, neither from the rich spots nor from the edges of the field where there is little crowding, but from situations where the environmental conditions are ordinary or even unfavorable. Individuals making

a good showing under such usual, or even adverse, conditions are worthy by *nature* rather than by *nurture* and are consequently most desirable as progenitors of future stock. By this method, as in that of Hallet, the attempt is not to keep the progeny of single individuals separate, but to mass together the best as they appear under ordinary normal environment.

This again is an indirect method of procedure, although the character of the germplasm is more nearly hit upon in this way than by Hallet's method, since the mask of temporary accessory modifications is stripped so far as possible from the somatoplasm, and the phenotype made to approximate the genotypical constitution.

B. PEDIGREE BREEDING

Mass selection, or the choosing of a number of individuals out of a population to be the progenitors of the next generation, is subject to repeated backsliding to mediocrity and consequently the selection must be made over and over again in each generation. A greater degree of success than is possible by this method has followed attempts to isolate single self-fertilizing individuals that manifest the desired qualities and to establish pedigrees from this isolated stock. This is Johannsen's method of the pure line and is particularly applicable to self-fertilizing plants, although it may be extended to clones, parthenogenetic lines and to homozygous crosses, as was pointed out in the last chapter.

The only way to get a pure line is to begin with a single source. This method is slow and laborious and will not replace mass selection in ordinary practice.

A quotation from the memoirs of the Manchu emperor K'ang-Hsi, 1662-1723, translated from *L'Empire Chinois,* E. R. Huc, will illustrate an early application of the pedigree

method. "On the first day of the sixth moon I was walking in some fields where rice had been sown to be ready for the harvest in the ninth moon. I observed by chance a stalk of rice already in ear. It was higher than all the rest and ripe enough to be gathered. I ordered it brought to me. The grain was very fine and well-grown, which gave me the idea to keep it for a trial and see if the following year it would preserve its precocity. It did so. All the stalks which came from it showed ear before the usual time and were ripe in the sixth moon. Each year has multiplied the produce of the preceding, and for thirty years it is the rice which has been served at my table. It is the only sort which can ripen north of the great wall, where the winter ends late and begins very early; but in the southern provinces, where the climate is milder and the land more fertile, two harvests a year may be easily obtained, *and it is for me a sweet reflection to have procured this advantage for my people.*"

In the last century the isolation of pure lines was practiced notably by the Englishman LeCoutour, who isolated 150 varieties of wheats, and by the Scotchman Shirreff who worked with various cereals.

In recent years the principle has been extensively applied with remarkable results, particularly by Nilsson of Svalöf in Sweden, who has employed this method since 1893, with peas, potatoes, clovers, grasses and grains.

Among others in America, Hays has isolated pedigrees of wheat at the Minnesota Agricultural Experiment Station which have been grown on thousands of acres and have "made possible the increased production of wheat throughout the northern States and Canada."

L. deVilmorin developed an isolation method that has been successfully applied to the sugar beet industry and has made

possible the profitable competition of continental Europe and the temperate United States with the cane-growing tropics.

The seeds from each plant to be tested are sown in separate beds from which upon maturity sample beets are taken and tested for sugar content. The plants from the bed furnishing the sample containing the highest percentage of sugar are then used as the seed producers for the next generation.

In this way the sugar content of beets has been raised from 6 per cent to 25 per cent or more, at which level it can be maintained by constant selection.

C. INBREEDING

When breeding is kept up between individuals of the same stock it tends to perpetuate or preserve the distinctive characteristics of that stock, a practice that was advocated in the Mosaic law—"Thou shalt not let thy cattle gender with a diverse kind; thou shalt not sow thy field with mingled seed." (Levit. XIX:19.)

Stock-breeders draw a distinction between inbreeding and so-called *line breeding*. Under "inbreeding" are included crosses which in human society would be regarded as incest, such as daughter by sire; dam by son; and sister by brother, while "line breeding" includes all other types of consanguinity within one line of descent.

Numerous experiments to test the effect of inbreeding have been carried out upon various organisms.

Darwin, for instance, planted morning-glories, *Ipomœa,* derived from the same stock of seeds, in two beds that were laid out side by side, that is, in an environment as nearly the same as possible, but with half of the beds screened from insects which usually transfer pollen from flower to flower. In the screened half where all insects were excluded the flowers

were of necessity self-fertilized, while in the exposed half they were presumably cross-pollinated by insects that had free access to them. The seeds produced in the two beds were kept separate and the experiment was continued for ten years, so that at the end of that time two lots of morning-glories, one self-fertilized for ten generations and the other presumably cross-pollinated for the same length of time, were obtained for comparison. The criterion Darwin used was the vigor of the plants as shown by the length of the vine. He found that the cross-pollinated plants were to the self-pollinated ones as 100 to 53, and such facts as this consequently led him to the generalization that cross-pollination is beneficial and self-pollination is detrimental.

Ritzema-Bos inbred rats for twenty generations. For the first ten generations the average number of young per litter was 7.5, while for the last ten generations it fell to 3.2.

Weismann inbred mice for twenty-nine generations and obtained a parallel result. For the first ten generations the average number per litter was 6.1, for the second ten generations 5.6, and for the last nine generations 4.2.

Dr. Helen King, on the other hand, has practiced close inbreeding with white rats for over 40 generations, comprising more than 20,000 individuals obtained by mating brothers and sisters from the same litter, at the end of which time the animals were larger and more vigorous than those not inbred.

Shull and East independently found in Indian corn, which occupies a larger area than any other cultivated plant in the United States, that loss of vigor results from continual self-fertilization, and many breeders have had similar experiences with animals as well as other plants.

In the case of the banana fly, *Drosophila,* Castle inbred

brother and sister for fifty-nine generations without diminishing the fertility of the line.

Hornaday cites the case of the deer in the royal herd at Windsor that arose from one male and two females introduced from New Zealand in 1862. The herd now numbers 20,000 and shows no signs of deterioration.

No arbitrary law with respect to the effects of inbreeding upon vigor and fertility can be laid down, therefore, which will apply equally to all cases.

"Inbreeding exerts its effects solely through the medium of inheritance and not through the blood-relationship of the individuals concerned" (Crew).

Nature has secured, often by elaborate devices, a separation of the sexes, especially among the higher organisms, and in consequence there has arisen an unavoidable necessity of outcrossing. The intricate adaptations existing between insects and flowers, for example, seem to be directed entirely toward insuring outcrossing among plants.

There are, on the other hand, various well known provisions in nature to insure inbreeding. The majority of plants are probably self-fertilized, while hermaphroditic animals, which sometimes at least are self-fertilized, particularly among the lower forms, are very frequent.

Among common plants wheat, barley, oats, rice, peas, beans, tobacco, and tomatoes are self-fertilized, and consequently homozygosity is established and weaklings tend to be eliminated.

The whole matter of inbreeding and the part it plays in emphasizing defects has received a fresh interpretation in the light of Mendelism.

There is a widespread popular belief that inbreeding is injurious and that it is necessary to outcross in order to main-

tain the vigor and avoid the defects of any line, but inbreeding in itself may not necessarily be injurious. The consequence of inbreeding as shown by the working of Mendelian laws is that latent or recessive characters tend to become homozygous and so brought to the surface, while outcrossing brings about the formation of heterozygous traits which mask recessive characters and render them ineffective.

In the case of mankind, consanguineous marriage of various degrees has long been forbidden by law or discouraged by custom in many races, particularly among the Jews, Mohammedans, Indians and Romans. On the other hand, the Persians, Greeks, Phœnicians and Arabs have freely practiced inbreeding, while one of the longest of known human pedigrees, the royal line of Egypt which produced the famous Cleopatra, was notoriously inbred, for at least four of the Ptolemys in this line are known to have married their own sisters and one his niece.

Incest, it will be recalled, is the familiar theme of more than one of the classical Grecian tragedies.

There has been a greater degree of inbreeding in the Puritan stock of New England than is commonly realized. David Starr Jordan points out that a child of to-day, supposing no inbreeding of relatives had occurred, would have had in the time of William the Conqueror, thirty generations ago, 8,598,094,592 living ancestors. If this theoretical supposition were really so, it would seem quite possible for every New Englander to-day to have at least one ancestral representative who won glory under William. The difference between the unthinkable number given above and the actual number of probable ancestors alive thirty generations ago emphasizes the fact that inbreeding must have occurred freely.

Cousin marriages, in which the blood of the grandparents

is again combined in the children, although producing a high percentage of defects, do not necessarily produce undesirable traits. They simply bring out latent or recessive characters for the reason that under these conditions similar defect may meet similar defect instead of the opposite allelomorphic normal condition which would dominate the defect and cause it not to appear.

Since a recessive trait may be properly regarded as the *absence* of a positive dominant character, it more frequently stands for an undesirable feature than otherwise. Thus it comes about that inbreeding, by combining negative features, may "produce" a defective strain.

Outcrossing always increases heterozygous combinations in the germplasm and covers up undesirable recessive traits through the introduction of additional dominant traits. Inbreeding, on the contrary, tends to simplify the germplasm, that is, to make it more homozygous, and so to bring recessive defects to the surface.

Inbreeding is "the detective that discovers the crime but not the criminal," as it simply allows natural selection to act on exposed recessive genes that tend to be covered up in outbreeding.

D. HYBRIDIZATION

Among the first to use the powerful tool of hybridization were Koelreuter (1733-1806) and Gaertner (1772-1850) in Germany, Naudin (1815-1889) in France, and Knight (1758-1838) in England. These pioneer transgressors of the Mosaic law cited in the foregoing paragraph, opened up a broad road to the army of Mendelians who were to follow them. Not only have individuals of two varieties showing hereditary differences been hybridized in nature but successful crosses have been artificially brought about be-

tween individuals belonging to different species, to different genera and even to different groups still more distantly related to each other.

It may be possible to point out at least two general methods of utilizing hybridization.

a. The Method of Burbank

This is a method of greatly increasing the number of variants by promiscuous hybridization and then of eliminating all except those of a desired phenotypic combination. Indirectly it depends upon the principle of the segregation of unit characters which makes possible *rearrangements* of these characters according to the laws of chance. The characters themselves remain unchanged, since nothing new is produced by hybridization except *new arrangements* of existing characters.

The spectacular success of Luther Burbank in "creating" new plant forms was due largely to his very extensive hybridizations, his skill in detecting among the varying progeny the winning phenotype in the living lottery and his ruthless elimination of the great majority of variations that did not quite fill his requirement.

Successful combinations must be propagated in most instances asexually by grafting, cuttings, bulbs, etc., rather than sexually through the medium of seeds, because new genotypes which will breed true are not necessarily isolated by this procedure. The consequence is that Burbank's method cannot be utilized in animal breeding to any great extent where the maintenance of a desirable strain by asexual propagation is out of the question.

It will be seen that this method, although commercially successful when practiced by a keen-eyed Burbank, is fortui-

tous and to a certain extent unscientific in that no one can repeat the exact conditions of the experiment and arrive at the same results. In the hands of a skillful plant breeder with unlimited resources at his command it may result in much practical achievement, but it does not particularly illuminate the path of other breeders who wish to repeat the experiment. It depends upon the chance mixing up of a large number of possibilities and then in not being distracted or blinded by the *good* while selecting the *best.* It is after all a selection of phenotypes and, therefore, forever open to error, since phenotypes do not always indicate what the behavior of their constituent genotypes will be in heredity.

b. The Method of Mendel

The method of Mendel, like the foregoing, depends upon hybridization with the difference that the desired combination is sought directly by definite *predetermined crosses,* according to the expectations of the Mendelian ratios, rather than through the random result of fortuitous combinations. It is a method which has been rendered possible by the determination of Mendel's laws of dominance, independent assortment and segregation of characters that give to the experimental breeder definite expectations and a method of procedure.

If, upon hybridization, the desired character behaves like a *recessive,* then all that is necessary to establish a pure stock exhibiting the character in question, is to breed two recessives together, because recessives are always homozygous and, regardless of their ancestry, breed true.

On the other hand, if the desired character proves to be a *dominant,* then it is necessary to determine whether it is present in a duplex or a simplex condition; in other words,

whether it is homozygous or heterozygous, for only homozygous organisms breed true. Establishing a strain consists, consequently, in making an organism homozygous.

The test to determine whether a dominant character is homozygous or heterozygous, that is, whether it will breed true or not, can be made by a single cross according to the procedure outlined in paragraph 8 of Chapter V. If upon crossing the individual to be tested with a recessive, it produces an entirely dominant progeny, then its germplasm is duplex for this character, and it will always reproduce the character in either duplex or simplex condition according to whatever cross may be made with it. When crossed, for instance, with another duplex dominant like itself, a pure homozygous strain of the character in question will be perpetuated.

If, on the contrary, the dominant character to be tested proves to be simplex or heterozygous, as determined by the fact that, when crossed with a recessive 50 per cent of the progeny are recessive, then it requires more than a single generation to establish a homozygous dominant strain.

In random inbreeding of diverse strains *if the recessives are constantly eliminated as they appear,* a population is gradually obtained which is composed of an increasing number of dominants so that after only a few generations the chances are much reduced that recessives will again appear, which means the practical purity of the strain.

E. GENOTYPIC SELECTION

The success, however, of any method of originating new types of organisms or of imposing old ones must depend in the long run upon somehow selecting germinal differences. The difficulty here of course lies in the fact that we may

only know the potential germplasm from its performance in producing somatoplasm, but Mendelism, with its analysis of the genes through breeding, has surely gone a long way toward making genotypic selection possible and definite. Moreover, the preservation and exploitation of mutations when they are known is certainly along the line of genotypic selection, since mutations when isolated may become the progenitors of desirable new lines. Accordingly, until the secret of the origin of mutations is solved, the work of the successful breeder consists to a very large extent in simply taking what mutations nature spontaneously furnishes to him rather than in attempting to force nature into producing something new.

5. Heterosis

When hybrids are formed the first hybrid generation not only shows more variability but also more vigor than the parental strains and this vigor is in proportion to the number of factors in which the parents differ, because in hybridization there is a pooling of hereditary resources. Such hybrid vigor is termed *heterosis*. Hybrids show heterosis when they have more dominant genes than either parent.

East and Hayes describe, for example, a cross between two different wild varieties of tobacco in which the average height of over fifty plants of each of the two wild parents was 31 and 54 inches respectively. Of an equal number of hybrids of the first generation the average height was over 67 inches under the same environmental conditions. Shull and East, working separately upon maize, came to the same conclusion, namely, that the first hybrid generation following an artificial cross is decidedly more vigorous than the parental stocks from which it is derived. This is shown in Figures 45 and 46.

Figs. 45 and 46.—Results of crossing two inbred strains of corn. At left in Figure 45 are two inbred varieties. The tall corn at the right is the result of crossing them. In Figure 46, below, the basket at the right represents the average production of two inbred strains after three generations of inbreeding—61 bushels per acre. The basket at the left shows the first generation results from crossing them—101 bushels per acre. After East and Hayes.

The mule is a notorious hybrid that possesses more "kick" than its parents.

Summarizing these results, inbreeding tends to stabilize the type and weaken the vigor of its individuals, while outbreeding or hybridization, on the contrary, weakens the constancy of the type but increases temporarily the vigor of its representatives.

"The only injury which may proceed from inbreeding comes from the *inheritance received*" (Jones).

CHAPTER X

THE CARRIERS OF THE HERITAGE

1. Introduction

Heredity, as has been shown in the introductory chapter, is essentially a matter of continuity between succeeding generations of living organisms. This continuity may be direct, as when a mother protozoan divides into two daughters, or it may be indirect, as illustrated by the relationship of a father and son, an uncle and nephew, or any other relatives of varying degrees of kinship which, taken singly or collectively, are somatoplasms derived in part from common streams of germplasm.

It is the purpose of the present chapter to consider this material continuity between succeeding generations and to discover, if possible, just what are the carriers of the heritage from one generation to another. To this end it will be necessary in the first place to recall what is meant by the "cell theory."

2. The Cell Theory

In 1838-1839 the "cell theory" of Schleiden and Schwann, which affirms among other things that all organisms, both plant and animal, are made up of cellular units, had its birth.

Robert Hooke, as early as 1665, had described "little boxes or cells distinguished from one another" that he saw in thin slices of cork, and to him is due the rather unfortunate use

of the term "cell" which has survived in biological writings to this day. The reason this term is unfortunate is because walls, which are ordinarily the characteristic feature of any cell, such as a prison cell, are usually the least important part of the structure of a living cell, often indeed being entirely absent.

3. A Typical Cell

A typical generalized cell is represented diagrammatically in Figure 47. Near the center of the cell the *nucleus,*

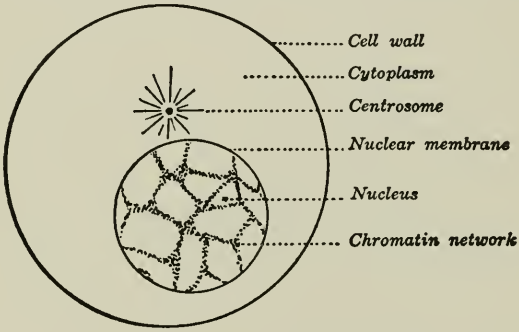

Fig. 47.—Diagram of a typical cell.

which Altenburg aptly describes as "like a lump of ice in water," is shown surrounded by a *nuclear membrane.* The nucleus, in common with the enveloping *cytoplasm,* is made up of living substance called *protoplasm* (Hugo von Mohl, 1846), and around the whole there is usually formed a *wall* or membrane that serves to separate one cell from another. Within the protoplasm there may be a considerable amount of non-living substance in the form of salts, pigments, oil-drops, water, and other inclusions of various kinds.

There may also be present in the cytoplasm of certain cells structures probably of organic nature, termed *mitochondria,*

the purpose of which is still a matter of controversy among cytologists, and in nerve cells, after proper staining technique, may also be displayed cytoplasmic *Golgi bodies* of unknown significance.

Plant cells are frequently equipped with packet-like *plastids* and *pyrenoids,* containing chlorophyll and starch grains respectively. All these organic inclusions arise from preceding structures of the same kind but their behavior during multiplication is not characterized by the predictable regularity that marks the propagation of nuclear parts, and consequently they probably do not play any important rôle in hereditary transmission.

The nucleus is to be regarded as the headquarters of the whole cell, since changes which the cell undergoes seem to be initiated in it, while cells deprived of their nuclei cannot long survive. A single instance will serve to show the vital part that the nucleus plays in the life-history of the cell. In 1883, Gruber found that after rocking a thin coverglass back and forth in a drop of water containing a collection of the protozoan *Stentor*, that has a long chain-like nucleus, these tiny animals could thus be cut into fragments, some of which recovered from the operation and regenerated into complete individuals. Only those pieces, however, which contained a fragment of the nucleus regenerate into new Stentors, while pieces of relatively large size which lack a fragment of nuclear substance very soon disintegrate.

The nucleus, it should be said, is made up of more than one substance, a fact that is easily demonstrated by processes of staining, in which certain dyes, through chemical union, stain a part but not the whole of the nuclear substance. The part most easily stained is called *chromatin,* that is, "colored material," and during certain phases of cell life the chroma-

tin masses together within the nucleus into visibly definite structures or bodies termed *chromosomes.*

Throughout all the various cells that make up the individuals of any one species these chromosomes appear to be practically constant in number and always in pairs, with some exceptions to be mentioned later in connection with sex, although the pairs usually differ particularly in size and shape from each other. This law of the constant chromosome number for any species was first stated by Boveri in 1900.

The chromosomes of different organisms vary in number from two in the worm *Ascaris* up to perhaps 1600, according to Haecker ('09), in certain radiolaria, where they appear as tiny granules. Chromosomes are the same in all cells of an organism and in all individuals of a species, with the exception of a difference in the sexes of certain species to be explained later. A list published a decade ago records the number of chromosomes known to be typical for 960 different animals.[1] Species which apparently are closely related may differ widely with respect to the number of their chromosomes, while species of unquestionably remote relationship may have an identical number of chromosomes in each of their cells. The number of chromosomes characteristic for a species, therefore, is in no way an index to the complexity or degree of differentiation of the species.

Practically nothing is known of the phylogeny of chromosomes, although there is every evidence that in their ontogeny they are always derived from preceding chromosomes.

The fact that chromosomes maintain their individuality apparently unaffected by either the metabolism, growth, or the reactions to stimuli of the cytoplasm in which they reside, although they play a definite rôle in controlling these activi-

[1] Jour. of Morphology, Vol. 34, pp. 1-67, 1920.

ties, is further evidence of the soundness of Weismann's "Germplasm Theory," and of the unlikelihood that somatic acquired characteristics can be handed on to succeeding generations by way of the germplasm.

Besides the nucleus there may often be identified in the cytoplasm of the animal cell a tiny body known as the *centrosome*. At certain times in the life-cycle of a cell the centrosome becomes the focal point of peculiar radiating lines, which play an important part in the behavior of the cell, particularly during the period of division.

Every cell passes through a cycle of life which may be compared with that common to individuals. It is born from another cell; passes through a vigorous youth characterized by growth and transformation; attains maturity when the metamorphoses of its earlier life give place to a considerable degree of stability; and finally, after a more or less extended period of normal activity, reaches old age, and death completes the cycle. In most instances, however, before this final phase is reached, the cell gives place to daughter-cells through fission, after the manner of most protozoans, and a new cell cycle is begun.

Sometimes the road of differentiation has been traveled so far that it is apparently impossible, as in the case of the complicated nerve-cells, to retrace these steps of differentiation and begin again. In such instances the outfit of cells provided in the embryo determines the numerical limit of the cells available throughout life. When this supply is exhausted no more cells appear to replace those that have been worn out.

4. Mitosis

The ordinary process by which two cells are made out of one is termed *mitosis*. It occurs constantly, and particularly

during growth, in all cellular organisms. A series of diagrams, modified from Boveri, illustrating the typical phases of mitosis is given in Figures 48 to 57.

Fig. 48. *The Resting Cell*

Fig. 49. *Beginning Prophase*

Fig. 50. *Early Prophase*

Fig. 51. *Prophase*

Fig. 52. *End of Prophase*

Fig. 53. *Metaphase*

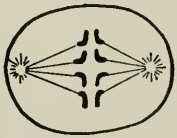

Fig. 54. *Beginning Anaphase*

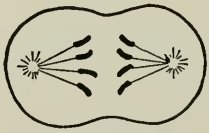

Fig. 55. *Anaphase*

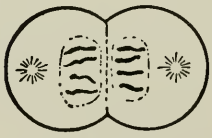

Fig. 56. *Beginning Telophase*

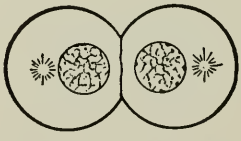

Fig. 57. *End of Telophase*

FIGS. 48-57.—Diagrams illustrating mitosis. After Boveri.

The resting cell (Fig. 48) is characterized by the presence of a nuclear membrane, a single centrosome, and by a chromatin network within the nucleus. In the *beginning of the prophase* (Fig. 49) the centrosome has divided into two parts, while in the *early prophase* (Fig. 50) the two centrosomes

have moved farther apart and definite separate chromosomes have formed out of the chromatin network. The *prophase proper* (Fig. 51) is marked by the vanishing of the nuclear membrane and by the more compact form of the chromosomes. At the *end of the prophase* (Fig. 52) the chromosomes have come to lie practically in one plane at the equator of the cell, being connected by "mantle fibers" with the centrosomes, each of which now occupies a polar position. In the *metaphase* (Fig. 53) the chromosomes split lengthwise, and at the *beginning of the anaphase* (Fig. 54) these half-chromosomes commence to separate from each other and to move toward the poles, while the mantle fibers shorten. During the *anaphase* (Fig. 55) the cell body lengthens and begins to divide, while the migration of the half-chromosomes toward the poles is completed. In the *beginning of the telophase* (Fig. 56) the half-chromosomes grow until they attain full size and the division of the cell body into two parts becomes complete. The mantle fibers have now disappeared and the nuclear membrane begins to reform around the chromosomes. Finally, at the *end of the telophase* (Fig. 57) the nuclear membrane becomes complete, the chromosomes break up into a chromatin network, and two resting cells take the place of the single one with which the process began (Fig. 48).

5. Sexual Reproduction

The mechanism by means of which two cells unite to make one in sexual reproduction is quite as complicated as that of mitosis by which one cell is transformed into two.

In sexual reproduction there are two kinds of germ-cells, the egg and the sperm respectively, which take part in producing a new organism.

They fit each other like a lock and key, in the sense that

the sperm fertilizes the egg of its own species and no other.

These cells are structurally unlike each other in nearly every particular, but each is a true cell, which von Kölliker made clear as early as 1841, and each has typically the same number of chromosomes in its nucleus, a fact more recently determined by van Beneden in 1883.

The egg-cell is often supplied with one or more envelopes of protective or nutritive function, and it is usually distended with stored-up yolk, in consequence of which it is comparatively large and stationary. The result is that whatever locomotion is necessary to bring the two cells together for union devolves upon the sperm-cell. Consequently the sperm-cells are practically modified into nothing but compact nuclei with locomotor tails of cytoplasm. They are, moreover, much more numerous than the egg-cells, so that although many go astray, never fulfilling their mission, the chances are nevertheless good that some one of them will reach the egg and effect fertilization.

Ordinarily only one sperm enters the egg, but when several succeed in penetrating into the egg-cytoplasm only one proceeds to combine with the egg nucleus, that is, usually only one sperm nucleus is normally concerned in the essential process of fertilization, a fact that was not definitely established until ten years after Darwin's "Origin of Species" appeared.

It was formerly thought by the school of "ovists" that in fertilization the essential process is a stimulation of the all-important egg by the sperm. The opposing school of "spermists," on the other hand, regarded the egg simply as a nutritive cell the function of which is to harbor the all-important sperm. It is now known that both the egg- and the sperm-cell are equally concerned in fertilization, which consists in the union of their respective nuclei within the cytoplasm of the egg.

6. Maturation

Certain preliminary changes of a preparatory nature, termed *maturation,* regularly precede the union of the nuclei of the two sex-cells in fertilization.

First of all it must be remembered that the chromosomes are present in the germ-cells, as well as in the somatic cells of the body, *in pairs,* being derived from two different parents. The behavior of these pairs in the germ-cells, however, is unlike that during mitosis in the somatic cells.

At the beginning of the maturation or preparatory processes in the germ-cells, homologous pairs of chromosomes conjugate, or come together in intimate contact with each other (*syndesis*). Later these partners separate and one complete set is segregated from the other so that two half groups are formed, each with an entire outfit of chromosomes made up of one chromosome from each pair.

These maturing changes result in reducing the outfit of chromosomes in each sex-cell to one-half the original number, a process that is necessary in order to maintain the chromosomal count which is characteristic for any particular species and which is known to exist unbroken from generation to generation. If there were no such reduction, then the fertilized egg, formed by the union of egg and sperm nuclei, would contain double the characteristic number of chromosomes, and during the formation of a new individual, the number in all the cells arising by mitosis from such a fertilized egg would likewise be double. If in turn the germ-cells of such individuals unite in fertilization, the original number of chromosomes would be quadrupled, and so on in geometric progression throughout subsequent generations. In 1883, too late for Darwin to learn of it, van Beneden discovered the all

important fact that the mature germ-cells, as expected, actually contain only one-half the normal number of chromosomes.

"When two parents transmit their characters, it is not the

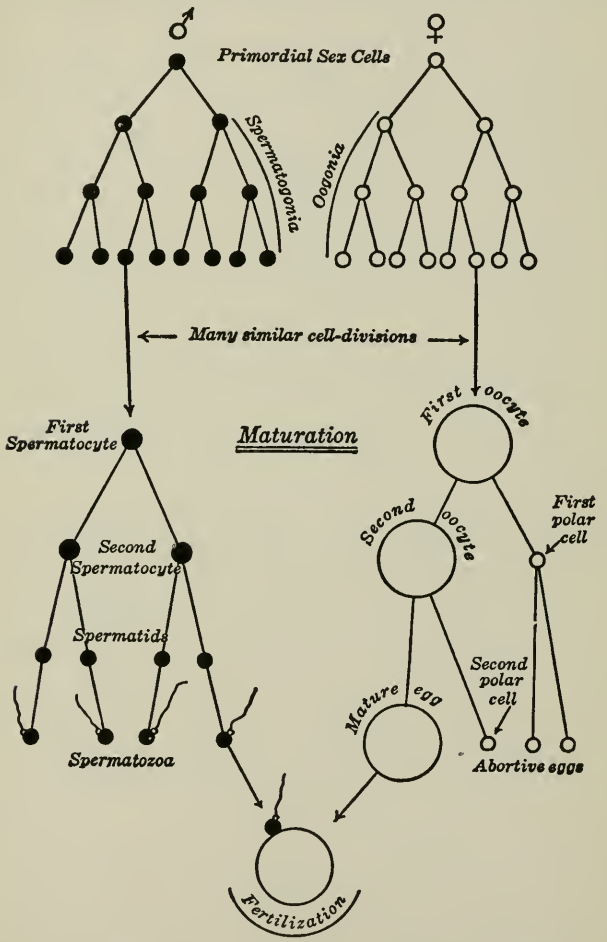

Fig. 58.—Diagram to show typical maturation and fertilization.

combined total of these characters that is transmitted in general, only half the combined total" (G. H. Shull).

The mature egg- or sperm-cell, with half its normal number of chromosomes, is termed a *gamete* (marrying cell), while the fertilized egg which is formed by the union of two gametes (mature egg- and sperm-cell), and which consequently has the characteristic number of chromosomes, is called a *zygote* (yoked cell).

A diagrammatic representation of the process of maturation is shown in Figure 58. The number of chromosomes (not shown in the diagram) remains constant in each germ-cell respectively until the division of second spermatocytes into spermatids that are subsequently transformed into sperm, and of the second oöcytes into mature eggs and second polar cells, when it is reduced to one-half the normal number. As spermatozoan and mature egg unite in fertilization, the original number of chromosomes is restored in the fertilized egg (zygote).

7. Fertilization

The stages concerned in a typical case of fertilization, according to Boveri, are illustrated in Figures 59 to 67.

In Figure 59 the "head" and the "middle piece" of the sperm-cell have penetrated into the egg cytoplasm, while in Figure 60 the tail of the sperm-cell has become lost and the middle piece, which furnishes the centrosome, has rotated 180° so that it lies between the nucleus, or head, of the sperm-cell and that of the egg-cell. Figure 61 shows an increase in the size of the sperm nucleus and a complete division of the centrosome into two parts that now begin to migrate toward the poles. This process of polar migration of the centrosomes is carried further in Figure 62 as well as the increase in the size of the sperm nucleus, until in Figure

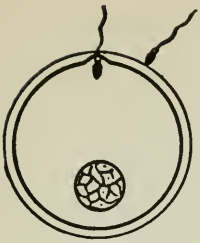

Fig. 59. *Entry of Sperm*

Fig. 60. *Loss of Sperm Tail*

Fig. 61. *Division of Centrosome*

Fig. 62. *Approach of Sperm Nucleus*

Fig. 63. *Increase of Sperm Nucleus*

Fig. 64. *Formation of Chromosomes*

Fig. 65. *Splitting of Chromosomes*

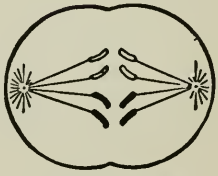

Fig. 66. *Anaphase*

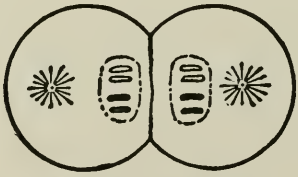

Fig. 67. *Two-celled Stage*

FIGS. 59-67.—Diagrams illustrating fertilization. After Boveri.

63 the process is complete so that the centrosomes have assumed a polar position and the sperm nucleus is equal in size to the egg nucleus and lies in contact with it. In Figure 64 the chromatin network of the two nuclei has formed into an equal number of chromosomes which in each case is half the number characteristic for the species. Figure 65 shows the complete disappearance of the nuclear membranes, a process that had already begun in the preceding figure, and also the arrangement of the chromosomes, connected with mantle fibers, in the equatorial plane where the former split longitudinally. In Figure 66, when the half chromosomes thus formed pull apart and migrate toward the poles, the segmentation or mitosis of the fertilized egg has begun, and there finally occurs, as shown in Figure 67, the two-celled stage following fertilization in which each cell contains the normal number of chromosomes, half of which came from the egg and half from the sperm.

8. Parthenogenesis

Fertilization is by no means always an essential process in the formation of a new individual, even in those animals which produce both eggs and sperm. Many animals and plants reproduce parthenogenetically, that is, the egg-cell may proceed to develop without first uniting with a sperm-cell. In these instances the chromosomes of the egg are not halved during maturation, and the offspring, therefore, continue to have the same number of chromosomes as the parent, since they are simply fragments of the parent.

Mead, Loeb and others, by the use of certain chemicals, succeeded in doing artificially what apparently is not ordinarily accomplished in nature, namely, making an egg that normally requires fertilization develop parthenogenetically.

9. The Hereditary Bridge

Whatever may ultimately prove to be determiners of the hereditary characters which appear in successive generations, it is obvious that, in any event, such determiners or genes must be located in the zygote, that is, in the fertilized egg. This single cell, therefore, is the actual bridge of organic continuity between any parental and filial generation. Moreover, it is the *only* biological bridge.

In the majority of animals the egg develops entirely outside of and independent of the mother, thus limiting to the egg-cell itself all possible maternal contributions to the offspring. Although there is abundant evidence that half of the filial characteristics come from the male parent, the only actual fragment of the paternal organism given over to the new individual is the single sperm-cell, which unites with the egg in fertilization, and the whole of this sperm-cell, even, is not usually concerned in the actual process of fertilization. The entire content of heritage is packed into the two germ-cells derived from the respective parents and, in all probability, into the nuclei of these germ-cells, since the nuclei are apparently the only portions of these cells that invariably take part in fertilization. To the new individual developing by mitosis from the fertilized egg into an independent organism, the factors of environment and response referred to in Figure 1, although absolutely essential, are subsequently added.

When it is remembered that the human egg-cell is only about $\frac{1}{125}$ of an inch in diameter, a gigantic size as compared with that of the human sperm-cell, and, furthermore, when one passes in rapid review the marvelous array of characteristics that make up the sum total of what is obviously

inherited in man, the wonder grows that so small a bridge can stand such an enormous traffic. A sharp-eyed patrol of this bridge as the strategic focus of heredity is proving to be one of the most effective points of attack in the entire campaign of genetics.

10. The Chromosome Theory

Certain investigators, who seek a morphological basis for heredity, regard the chromosomes as the carriers of the heritage. In other words, they are the source of the determiners of ontogeny or the effective factors in the process of differentiation.

A few of the grounds for this theory are briefly indicated below.

First: In spite of the great relative difference in size between the egg-cell and the sperm-cell, in heredity the two are practically equivalent, as has been repeatedly shown by making reciprocal crosses between the two sexes. The only features that are apparently alike in both the germ-cells are the chromosomes. The inference is, therefore, that they contain the genes which are the causal factors for the equivalence of adult characters in heredity. The existence of an extra chromosome in probable connection with the matter of sex is, as will be pointed out later, an exception to the exact chromosome equivalence of the two sexes, which only goes to strengthen the supposition that the chromosomes are the carriers of hereditary qualities since extra chromosomes are always associated with the character of sex.

Second: The process of maturation, which always results in halving the chromosome material of the germ-cells as a preliminary step to fertilization, is a series of complicated manœuvers not practiced by other cells. During this process

no other part of the cells appears to play so consistent and important a rôle as do the chromosomes. Provided they act as hereditary carriers, their peculiar behavior during maturation is just what is needed to bring together an entire complement of hereditary determiners out of partial contributions from two parental sources.

Third: Sometimes abnormal fertilization occurs, as in the case when two or more sperm-cells, instead of one, enter the egg cytoplasm and unite with the egg nucleus. This unusual performance has been artificially induced by chemical means in the case of sea-urchins' eggs. The fertilized egg, or zygote, thus formed with an excess of male chromosomes, results in the development of abnormal larvæ. It is thought that a causal connection may exist, therefore, between the additional male chromosomes in the fertilized ovum and the abnormalities of the progeny.

Fourth: The fact that chromosomes may retain their individuality throughout the complicated phases of mitosis, as has been proven in some instances, agrees with the corresponding fact that certain characteristics of the somatoplasm maintain their individuality from generation to generation.

Moreover, certain chromosomes in the fertilized egg have been identified with particular features in the adult developing from that egg. Tennent, for example, summarizes his work on Echinoderms (1912) by the statement that from a knowledge of the chromosomes in the parental germ-cells, particular characters in the adult hybrids may be predicted, and, conversely, that from the appearance of sexually mature hybrids the character of certain chromosomes in their germ-cells may be predicted.

Again, the correlation of a particular chromosome in the germ-cells with a definite adult character, namely sex, has

been repeatedly demonstrated in connection with the so-called "extra chromosome," already referred to.

Fifth: Finally, excellent evidence of a definite causal connection between certain chromosomes of the germ-cells and particular somatic characters has been furnished by crucial experiments upon the eggs of sea-urchins. Boveri found that he was able in some instances to shake out the nuclei bodily, chromosomes and all, from the mature eggs of the sea-urchin, *Sphœrechinus,* and when there was added in sea water to such enucleated eggs the sperm-cells of an entirely different genus of sea-urchin, namely, *Echinus,* the *Echinus* sperm-cells entered the *Sphœrechinus* eggs, which had been robbed of their nuclei, and from this combination larvæ developed exhibiting *only* characters peculiar to *Echinus.*

Such cumulative circumstantial evidence as the foregoing has convinced many that in the chromosomes we have visibly before us the carriers of heredity.

In any event the supposition that the chromosomes, with certain chemical reservations, are the morphological carriers of the heritage, forms an excellent working hypothesis, and this chapter may suitably be closed with a quotation from E. B. Wilson, whose brilliant work in the entire field of cytology makes it possible for him to speak with authority. "In my view studies in this field are at the present time most likely to be advanced by adopting the comparatively simple hypothesis that the nuclear substances are actual factors of reaction by virtue of their specific chemical properties; and I think that it has already helped us to gain a clearer view of some of the most puzzling problems of genetics."

Sutton in 1902 was the first one to point out how the chromosomal apparatus supplied the necessary mechanism to account for Mendelism.

CHAPTER XI

THE ARCHITECTURE OF THE GERMPLASM

1. Drosophila, the Biological Cinderella

Just as the bacteriologist firmly believes that guinea pigs were specially created for serological experimentation, so the geneticist has come to realize that the banana fly, *Drosophila melanogaster,* to which repeated reference has already been made, was designed for disclosing the secrets of the "architecture of the germplasm" (Weismann).

This tiny ubiquitous fly (Fig. 32), which hovers around bruised fruit without regard to place, is so small and harmless that it does not even qualify as a pest. It has proved, nevertheless, to be a veritable bonanza to the geneticist. It has many well-defined characters that can be observed under the microscope and it lives successfully upon a bit of banana in a milk bottle plugged with cotton. Every ten or eleven days a pair produces two to three hundred descendants which in turn are ready to produce similar families of their own, so that the investigator who begins with them needs to be an expert bookkeeper in order to be able to record his results. Although, like Cinderella, *Drosophila* comes from the humble environment of the garbage can, yet this fly has easily outstripped all its sister competitors for genetical honors, until to-day it stands probably as the most famous experimental organism in the whole world.

Prof. T. H. Morgan, formerly of Columbia University and

now director of the Kerckhoff Laboratories of the Biological Sciences at the California Institute of Technology at Pasadena, is the most conspicuous leader in the investigation of *Drosophila*. In his laboratory over ten millions of these animals, which literally "breed like flies," have passed in review under the microscope while pedigrees of over three hundred generations have been obtained and recorded. In no other animal or plant has the remarkable parallelism between the segregation of Mendelian characters in experimental breeding and the behavior of the chromosomes been so completely demonstrated.

2. Linkage

Drosophila has only four pairs of chromosomes although more than four hundred different characters have been found in the flies themselves, a fact which makes it at once evident that many genes, or character-determiners, must be located together in each chromosome.

Experimental breeding of *Drosophila* shows that there is not always complete independent assortment of the different characters that enter into a cross, such as Mendel found to be true for the different characters of peas with which he experimented.

Genes located together in any one chromosome are likely to stay together even during the conjugation of the chromosomes and the subsequent separation of the members of homologous pairs in the process of maturation. This hanging together of neighboring genes of the same chromosome throughout the complicated process of meiosis or maturation is termed *linkage*.

It is extremely fortunate for the evolution of our knowledge of the mechanism of heredity that Mendel happened to work upon characters the genes of which are located in separate

chromosomes, and so was able to establish the law of the independent assortment of unit characters before the apparent contradiction, called linkage, became known. If he had come upon the confusing phenomenon of linkage first, the discovery of the laws of Mendelism, in all probability, would have been long delayed.

Bateson and Punnett called attention to linkage as early as 1906 under the name of "coupling" in the case of certain characters of sweet peas. A vague general knowledge of many groups of correlations, such as deafness and defective teeth going along with blue eyes and albinism in cats, had for a long time existed.

In *Drosophila,* the brilliant and extensive investigations of Morgan and his co-workers have resulted in definitely placing over two hundred known characters in four linkage groups corresponding to four pairs of chromosomes. The limitation of linkage groups to the number of chromosome pairs found in the organism is proving to be one of the fundamental principles of heredity.

Moreover, it has been shown by reciprocal crosses that linkage when it occurs is not due to some relation *per se* between the genes but simply to the fact that the linked genes chance to lie together in the same chromosome. In other words, if two characters enter a cross together from one parent they will stay together in the offspring, and if they enter from separate parents they remain separate in the offspring.

3. The *Modus Operandi* of Linkage

The way linkage works out may best be made clear by illustrations from Morgan. When an ordinary wild-type fly with *gray body* and *long wings* is crossed with a fly showing the two mutations of *black body* and *vestigial wings,* the hy-

brids of the first generation are all like the wild-type parent because gray body and long wings are dominant over black body and vestigial wings.

When a *male* of one of these hybrid flies is crossed back

Female gametes \ Male gametes	*GL*	*Gv*	*bL*	*bv*
bv	*GL* / *bv*	*Gv* / *bv*	*bL* / *bv*	*bv* / *bv*
bv	*GL* / *bv*	*Gv* / *bv*	*bL* / *bv*	*bv* / *bv*
bv	*GL* / *bv*	*Gv* / *bv*	*bL* / *bv*	*bv* / *bv*
bv	*GL* / *bv*	*Gv* / *bv*	*bL* / *bv*	*bv* / *bv*

FIG. 68.—Checkerboard to show the result of crossing a gray-long, black-vestigial hybrid male fly back to a black-vestigial recessive female. G = gray body; L = long wings; b = black body; v = vestigial wings.

with a recessive black-vestigial *female, if Mendelian segregation took place* there ought to be four possible kinds of offspring in equal numbers, as shown in Figure 68, viz., gray-long; gray-vestigial; black-long; and black-vestigial. The actual experiment, however, shows but two classes of offspring, viz., gray-long and black-vestigial, like the two grandparents

(Fig. 69). In other words, gray body and long wings entering the cross from one parent stay linked together as do also black body and vestigial wings. Crossing a hybrid back to the

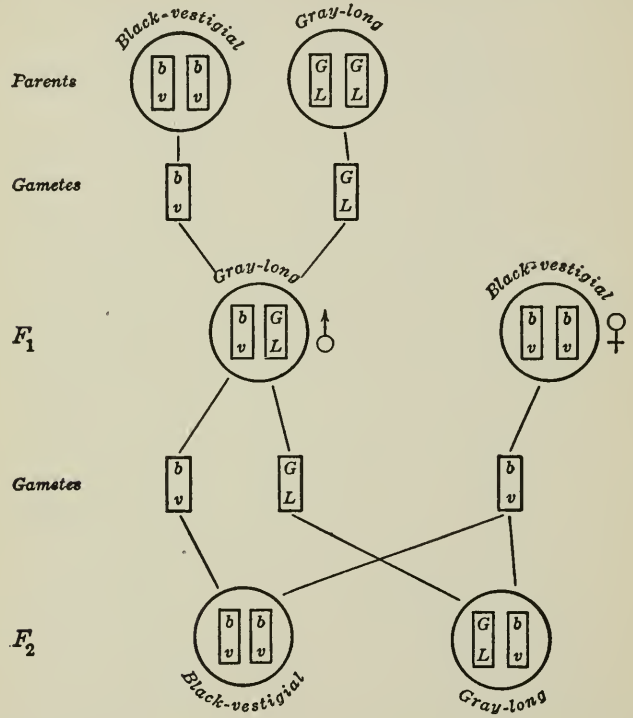

FIG. 69.—Typical linkage in *Drosophila*. Symbols as in Figure 68. Data from Morgan.

recessive is the common procedure in order to bring out what is latent in the hybrid, for the recessive, since it does not dominate or conceal anything, allows whatever is present in the hybrid being tested to appear.

The Mendelian practice of crossing the F_1 hybrids together

tends to conceal linkage and perhaps has prevented its earlier recognition.

The reciprocal cross is shown in Figure 70. In this case,

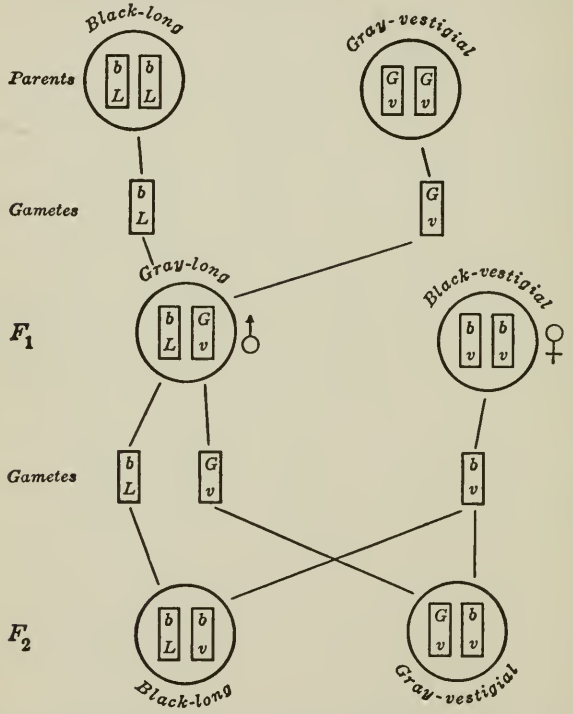

FIG. 70.—Typical linkage in *Drosophila*. Reciprocal to the case shown in Figure 69. Data from Morgan.

likewise, whatever goes in together comes out together and no new combinations appear.

4. CROSSING-OVER

On the other hand if a gray-bodied long-winged *female* hybrid, such as is produced in the preceding experiment by

crossing gray-long and black-vestigial together, is crossed back to a recessive black-vestigial *male,* there are produced four kinds of offspring, gray-long and black-vestigial like the grandparents and two new combinations, gray-vestigial and black-

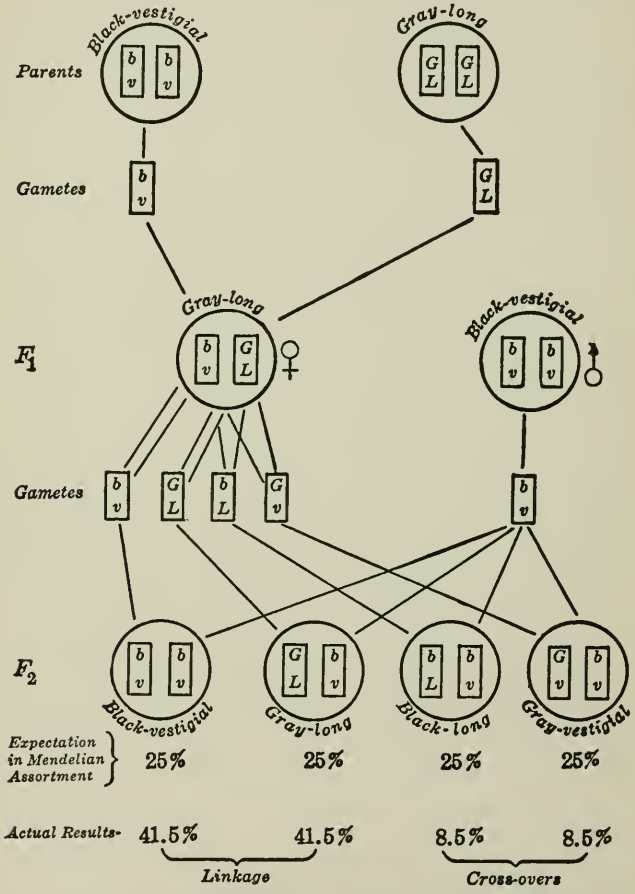

FIG. 71.—Typical crossing-over in *Drosophila.* Symbols as in Figure 68. Data from Morgan.

long. These four types of F_2 are what would be expected upon free assortment of all the gametes and they should all occur in equal numbers or in the proportion of 1 : 1 : 1 : 1. See Figure 68. Instead, as an actual result of extensive and repeated crosses of this kind, Morgan obtained 41.5% each of gray-long and black-vestigial and 8.5% each of the new combinations of black-long and gray-vestigial (Figure 71). The new combinations represent *crossing-over* or breaks in the linkage of the genes within the chromosomes.

Although this superficially resembles the free independent assortment of typical Mendelian crosses, it is quite a different thing, since independent assortment involves whole chromosomes while crossing-over involves only parts of chromosomes. The theoretical ratio of the different classes resulting in the F_2 generation from hybrids is different in typical Mendelian assortment and in crossing-over. In the former case when the hybrids are crossed *inter se* it is 9 : 3 : 3 : 1, while in the latter, when the hybrid is back-crossed with the recessive, it is 1 : 1 : 1 : 1.

Furthermore, the actual percentage of cross-overs varies in different crosses. For example, when white-eyed yellow-bodied flies are crossed with normal wild-type red-eyed gray-bodied individuals, the resulting hybrids resemble wild red-eyed gray-bodied flies. When such a female hybrid is crossed back to a recessive white-eyed yellow-bodied male, the offspring show only 1% of crossing-over, that is, white-eyed gray-bodied and red-eyed yellow-bodied individuals, and 99% of linkage, that is, white-eyed yellow-bodied, and red-eyed gray-bodied flies (Fig. 72).

Another percentage of crossing-over, that between white-eye and miniature-wing with red-eye and normal-wing, was found to be 33. It is obvious from Fig. 71, that in any case the cross-

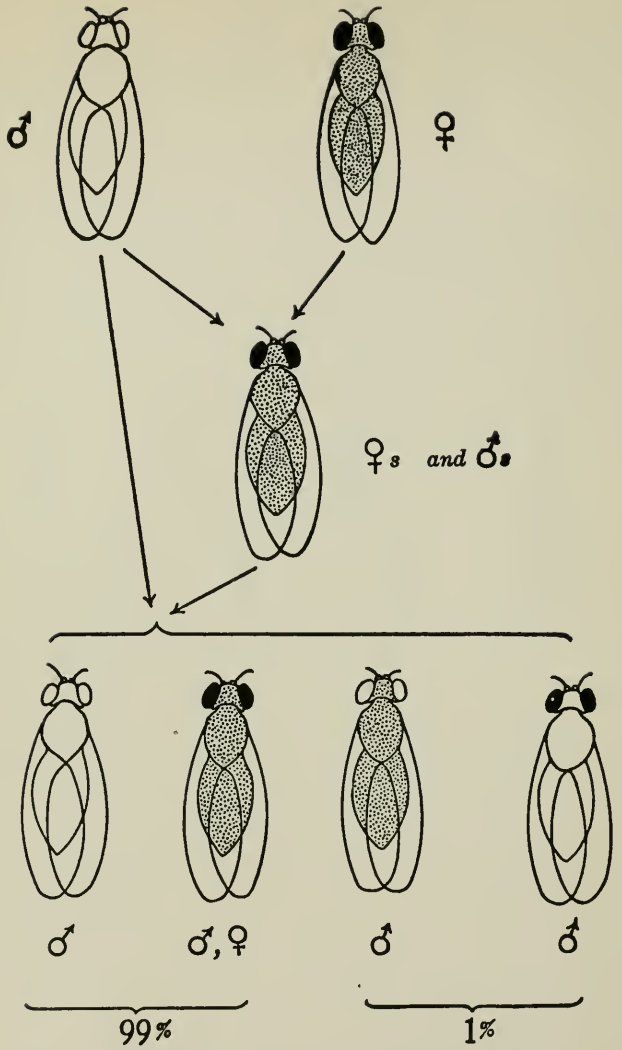

FIG. 72.—A case of one per cent crossing-over in *Drosophila*. Gray-body and red-eyes are represented by stippling and solid black respectively. Yellow-body and white-eyes are unshaded. After Sharp, from Morgan's data.

ing-over will never exceed 50% if the four kinds of gametes of the hybrid female are produced in equal numbers.

5. How Does Crossing-over Occur?

In germ-cells before maturation, homologous maternal and paternal chromosomes pair off and usually come to lie side by side. This is the phenomenon, already described, of *syndesis* or conjugation. During this temporary contact of homologous chromosomes there seems to be an opportunity for an ex-

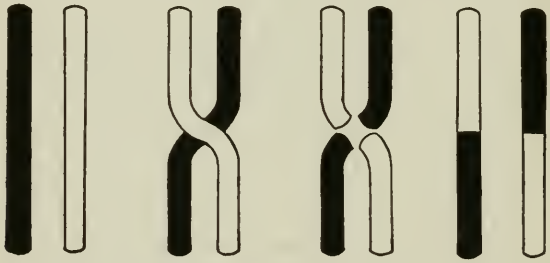

Fig. 73.—Diagram to show crossing-over between two homologous chromosomes. After Muller.

change of parts such as the results of breeding demonstrate does actually occur.

Syndesis has been repeatedly observed under the microscope and sometimes two chromosomes of an homologous pair have even been seen to twist about each other. When separation comes after this embrace the two original chromosomes may simply unwind and so regain their former identity unchanged, or they may fuse and break in such a way that one (in solid black) has a part of the other (in outline), and the remaining parts show a corresponding reciprocal union, as indicated in Figure 73.

This is the chromosomal explanation (*Chiasma-type theory*

of Janssens) of the crossing-over phenomena known to the experimental breeder.

Probably crossing-over occurs in homozygotes as well as in hybrids but there is no way to detect it.

Jennings has said: "The studies of 'crossing-over' promise to bring us into closer touch with the actual details of the hereditary mechanism than any other phenomena now under examination."

6. Interference

The varying percentages of crossing-over between different pairs of genes led Morgan and his associates to attempt the localization of genes within the chromosomes. The idea is simply this, that the farther apart two genes are in the chromosome the more likely they are to cross over and to exchange places with their homologous genes during syndesis.

Of course if they lie very close together in the chromosome they are apt to be found finally on the same side regardless of the twisting of the paternal and maternal chromosomes about each other and the subsequent realignment of their parts. This is evident in Figure 74 where the invisible genes are represented hypothetically by letters placed within the chromosomes. Crossing-over is more likely to occur between A and E which lie at the extremes of chromosome I than between A and B which are closer together.

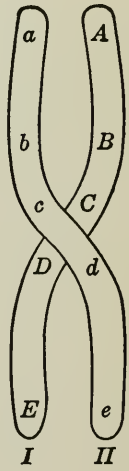

Fig. 74. — Interference. Two homologous chromosomes during syndesis. When there is a crossing-over between Cc and Dd, it *interferes* with another crossing-over near by between Cc and Bb.

Again, when genes lie close together they theoretically interfere with the crossing-over of neighboring genes as pointed out by Muller and confirmed by subsequent breeding experiments. In Figure 74, for example, if crossing-over took place between the pairs Cc and Dd, breaking the linkage between C and D and between c and d, it would prevent another break of linkage between BC and bc. This is the phenomenon of *interference*. It follows that the nearer together two pairs of genes involved in crossing-over are located, the greater will be the interference.

It is furthermore apparent that it is not single genes alone that are involved in crossing-over but whole blocks of genes.

7. The Arrangement of the Genes

Breeding experiments show definite percentages of crossing-over, therefore genes have a fixed locus within the chromosome and are not distributed in a hit-or-miss fashion.

The percentages of crossing-over, consequently, may be taken as an indication of the *distance* of the genes from each other.

Morgan assumes, for example, that if one per cent of crossing-over occurs this may be taken to represent one *arbitrary unit of distance* between the two genes in question. Haldane proposes to call this unit of crossing-over a *morgan,* and Crew and others have adopted the term. In the illustration of black body and vestigial wing, where there was 17% of crossing-over, it is assumed that the genes for these two characters are 17 units (or morgans) apart in the chromosome.

Following up this fertile idea it becomes possible to map even the exact location of the genes in the chromosomes. The existence of the genes themselves is directly deducible from breeding experiments, regardless of what their exact location

may be. Sturtevant was the first to make such a map for the genes in the "sex chromosome" of *Drosophila.*

This has been followed by maps of the other chromosomes, after the breeding of a total of several million flies and the analysis of the data which include altogether the behavior of over a hundred different genes. It should be noted in this connection that the arrangement of the genes in the chromosomes bears absolutely no relation to the arrangement or proximity of the parts of the body affected by the genes.

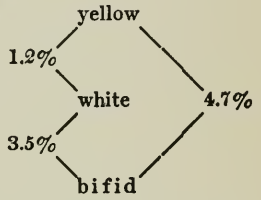

FIG. 75.—An illustration of the proof of gene-localization from crossing-over percentages obtained by actual breeding of banana flies.

The *relative location* of the genes has been determined by the following method: If, for example, two genes, A and B, upon breeding back to the recessive show 5% of crossing-over with a and b, while B and C show 20% with their allelomorphs, b and c, then when A and C are bred together with a and c, they should give either the sum (5 + 20 = 25%) or the difference (20— 5 =15%) of crossing over.

For example, in an actual experiment, yellow-body and white-eye gave 1.2% of crossing-over while white-eye and bifid-wing gave 3.5% of crossing-over. When yellow-body and bifid-wing were tested they met the expectation and gave 4.7%, or the sum of the other two percentages, as shown in Figure 75.

If upon breeding yellow and bifid a percentage of 2.3% had been obtained instead of 4.7% as was actually found, then the order of the genes would have been bifid-yellow-white instead of yellow-white-bifid.

In the eloquent frontispiece of "The Mechanism of Men-

delian Heredity," by Morgan, Sturtevant, Bridges and Muller, there are drawn four straight parallel lines representing the "chromosome maps" of *Drosophila* as known in 1915. It is doubtful if in any book there may be found four straight lines that mean so much. The work of gene-localization is quite comparable to that done by mathematicians and astronomers in determining the distances that separate the stars in the heavens from each other and is perhaps equally incomprehensible to the layman.

In gene-localization it is the infinitely small instead of the infinitely great that one must compute. When it is remembered that *Drosophila* is a very tiny fly; that paired reproductive organs occupy only a small part within its abdomen; that each of these reproductive organs in the male is made up of several tubules; that within these tubules may eventually be found the sperm-cells with plenty of room to move about; that within a single sperm-cell is the nucleus; that after half of the contents of the nucleus has been disposed of there remain four chromosomes; that within each chromosome there are beyond the range of vision hundreds of genes and that it has been possible in a single chromosome to determine not only the relative arrangement of over thirty genes but also to find out the relative distance between these genes, it will be realized that the analysis of the germplasm has gone a long way.

In Figure 76, taken from Morgan's "Theory of the Gene," are represented the four chromosome maps of *Drosophila* corrected to 1926 to show the linear arrangement of the genes in the chromosomes.

The four visible chromosomes of *Drosophila* correspond to the four linkage groups of characters obtained by experimental breeding and it is a striking fact that no character has yet

appeared that cannot be assigned to one of these four linkage groups. The relative length of the four "maps," which has

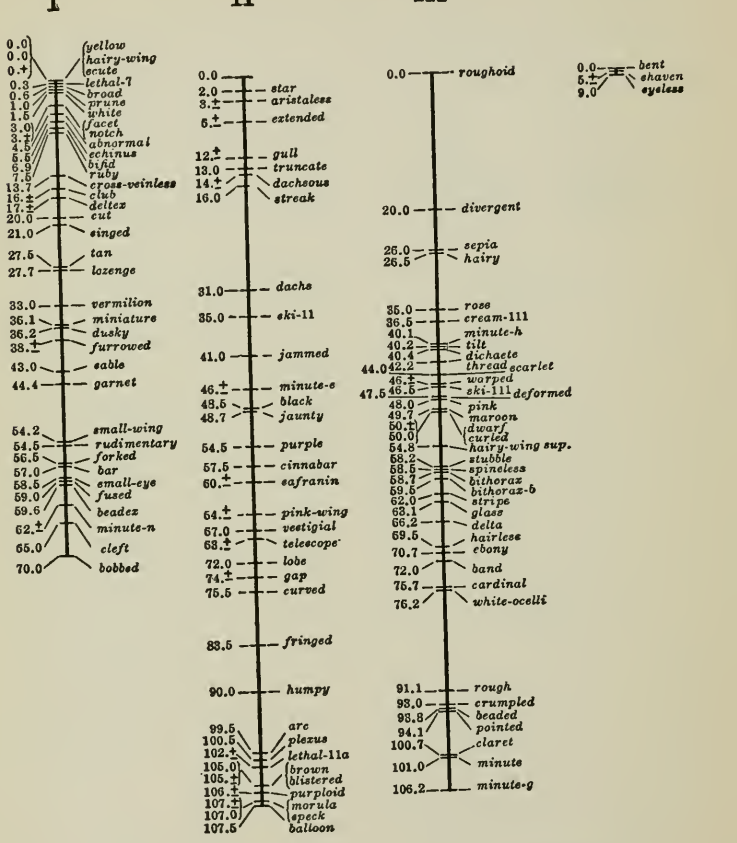

FIG. 76.—Chromosome maps of *Drosophila*. After Morgan.

been determined from the carefully worked-over data acquired by years of riotous breeding for crossing-over, agrees remarkably with the relative differences in the actual size of the

chromosomes as measured under the microscope. The four pairs of chromosomes in *Drosophila melanogaster* are represented in Figure 77.

While crossing-over is confined to the female in *Drosophila,* possibly because syndesis is interfered with in the male on account of the unlikeness of the XY chromosome pair, it is known to occur in both sexes in some other forms, for example, in the grouse locust, primrose, maize and rat.

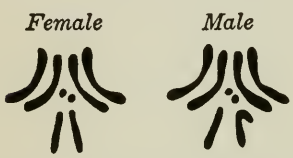

Fig. 77.—The chromosomes of *Drosophila melanogaster.* After Bridges.

Castle has summarized the chromosome theory of linkage in the following compact manner:

"1. Genes which show linkage with each other are located in the same pair of chromosomes. It is the substance of the chromosomes which binds the genes together and causes *A* to be inherited when *B* is.

2. Genes close together in the same chromosome show strong linkage, genes farther apart show less linkage.

3. Homologous chromosomes, those containing corresponding sets of genes, one set derived from the father, one from the mother, lie side by side (in synapsis) previous to the formation of the gametes. At this time breaks are likely to occur in the chromosomes and parts of one are likely to replace corresponding parts of the other.

4. Such replacement is called crossing-over.

5. Breaks occur more commonly in long chromosomes than in short ones, and between distant points on the same chromosome.

6. The genes occur in a chromosome, like beads on a string, in a single row and in definite order."

8. Linkage in Other Organisms

The phenomenon of linkage has already been observed in various other organisms besides *Drosophila*. Even in Mendel's classic peas, White demonstrated four linkage groups of characters and seven pairs of chromosomes. It is doubtful if Mendel himself ever heard of chromosomes, for he died in 1886, and Boveri's pioneer work on chromosomes had only then recently appeared. A list of a few of the organisms in which linkage has been reported is given below.

Organisms that show linkage	*Author*
Pea	White
Sweet pea	Bateson and Punnett
Snapdragon, Wheat	Baur
Primrose	Altenburg. Gregory
Maize	Emerson. Breggar. Lindstrom. Jones
Rice	Chao
Tomato	Jones. MacArthur
Beans. Oats	Surface
Barley	Robertson
Evening primrose	Shull
Morning Glory	Imai
Drosophila virilis " busckii " repleta	Metz
Silkworms	Tanaka
Grouse locust	Nabours
Top minnow	Gordon and Frazee
Pigeon	Cole and Kelly
Fowl	Warren
Mouse	Castle and Dunn. Detlefsen. Feldman
Rat	Ibsen. Dunn. Castle
Rabbit	Castle

No organism has been found in which the number of linkage groups exceeds the number of chromosomes.

CHAPTER XII

SOMATOGENESIS

1. The Hereditary Tunnel

The earlier studies in heredity up to the end of the 19th century were concerned with the comparison of successive individuals, or somatoplasms. This phenotypic method has attained a considerable degree of success through the analysis afforded by Mendelism.

A different and still more recent method of attack upon the problem of heredity deals not with individuals but with chromosomes which are generally acknowledged to be the living springs from which flow the streams of inheritance. Such an intensive cytological study of the germplasm has revealed a mechanism that explains to a marvelous extent the results of the experimental breeder.

The demonstration of the close parallel between the behavior of the germplasm as seen in the chromosomes and the performance of the somatoplasm as exhibited in the end results of experimental breeding, is one of the most impressive scientific achievements of our times.

There is an undoubted causal connection between the genotype and the phenotype at the extremes of the hereditary pageant but between these extremes, that is, between the fertilized egg and the adult, investigators are as yet by no means as confident or well-informed. It is as if heredity was represented by a long underground tunnel. We are in the light

at either end and have made out to a considerable degree the details around the entrance and the exit, but we are still largely in darkness throughout the passageway itself.

"Heredity is simpler but the problem of development is more complex than in Darwin's time. From germ cell to adult an almost infinitely complex series of interactions of elements must take place and something may happen all along. The difficulty in the study of heredity is that the character in the germ cell must be deduced from the study of variation in the character at the other end of the developmental history" (Sewall Wright).

The science of embryology has given us a series of flashlight pictures of what goes on in the tunnel of development but of necessity its contribution has been largely morphological. Consequently the geneticist still awaits some torch-bearer who will reveal how an invisible gene within a chromosome can give form and substance to a definite visible character in an organism. Probably genetics has contributed more to embryology than embryology to genetics in the past but it is quite likely that the account will be more than balanced in the future.

The way in which germ-cells come by their potent hereditary components, rather than how they make use of them, has been the first and most natural problem to engage the attention. The solution which satisfies most biologists, who have considered the evidence, has been found in the idea of the *continuity of the germplasm,* that is, that hereditary genes are not the product and result of the body carrying them but are lineal descendants of ancestral genes which have been housed temporarily in other bodily domiciles in the past.

The familiar miracle of how hereditary genes work together to produce a new plant or animal is farther from a satisfac-

tory solution, yet there is no doubt that some of the impending great discoveries in genetics are sure to be exactly in this field.

2. Preformation and Epigenesis

How does germplasm transmute into somatoplasm?

Historically there have been two conspicuous attempts to solve the riddle of differentiation, neither of which gives intellectual satisfaction any longer in the light of what is known to-day.

The first held sway in the 17th and 18th centuries under the guise of the *preformation hypothesis* which assumes that development is simply the unfolding and enlarging of what was already present in the germ in miniature. This has been called the theory of "infinite encasement," because, not only is the miniature plant or animal supposed to be packed within the germ-cell like the embryo plant between the cotyledons of the bean seed, but within each miniature also it is supposed that the minute representative of the next generation is encased, and the next, *ad infinitum*. Aided by a poor microscope and a good imagination the idea of preformation was carried to such an extreme that a mannikin or "homunculus" was actually figured by Hartsoeker seated within the head of a human spermatozoan.

A modern intellectual cousin of the preformation hypothesis is the suggestion of Bateson that since most mutations involve the *loss* of some character the logical inference is that the farther back in evolution one goes the more characters are to be found in the germplasm and that consequently man represents a sort of a simplified *Ameba*.

The second attempt to solve the riddle of development resulted in the hypothesis of *epigenesis* which goes to the other extreme, maintaining that organization gradually appears

out of an absolutely simple undifferentiated germ. This hypothesis had its most influential exposition in "Theoria Generationis" by C. F. Wolff in 1759.

"The mistake in the doctrine of preformation was in supposing that germinal parts were of the same kind as adult parts; the mistake of epigenesis was in maintaining a lack of specific parts in the germ" (Conklin). Neither of these two conceptions is in accordance with the facts as known to-day.

3. What Is Somatogenesis?

Development is not simply the unfolding or assortment of what is already present in the germ nor is it the miraculous writing of something new upon a clean slate. Rather it is the orderly initiation and sequence of new structures and functions conditioned by the interaction between the germinal elements present in the fertilized egg or ovule and its environment.

Thus *somatogenesis* is the study of the emergence under favorable surroundings of bodily structure out of hereditary sources. Like the evolution of species, which has so enthralled the minds of thinking men, somatogenesis in a parallel way is the evolution of the individual. No doubt each of these epic histories will eventually furnish the key and vocabulary to the other.

As Conklin has well said, "The development of a human being, of a personality, from a germ cell is the climax of all wonders, even greater than that involved in the evolution of a species or in the making of a world."

Both somatogenesis, or the rise of the body, and gametogenesis, which concerns the origin of the germ-cells themselves, are cytological in their terminology, and are referable to the germplasm, as contrasted with the Mendelian and

biometric aspects of genetics which are not primarily cytological but are, on the contrary, statistical in method, dealing directly with somatoplasms (Fig. 78).

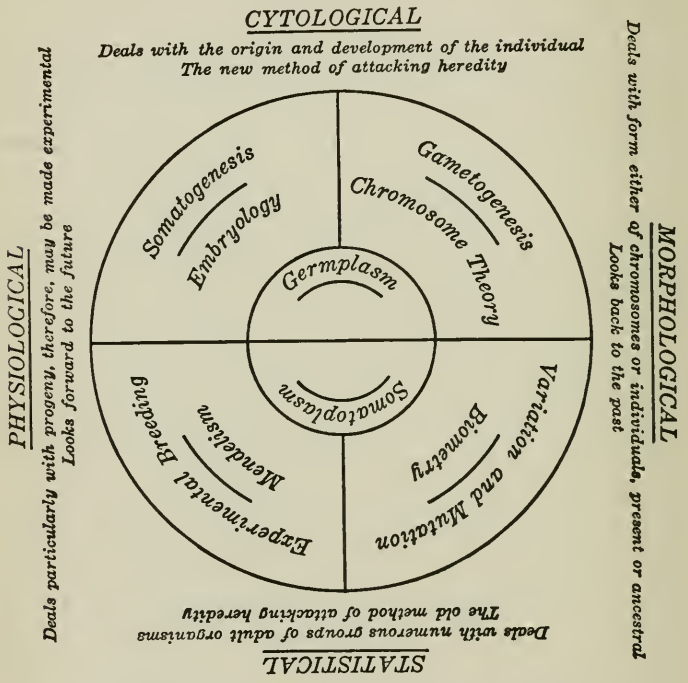

Fig. 78.—Any-side-up diagram of Genetical Sciences.

4. The Factors in Somatogenesis

Somatogenesis deals necessarily with the interaction of at least two sets of factors, viz., hereditary, and environmental. In higher animals particularly a third factor, "response" (see Fig. 1), may be added.

Hereditary factors have been described and have received the major share of attention in the preceding pages. Environ-

mental factors may upon occasion, however, cause enormous modifications in somatogenesis although the limits of variation are set by hereditary genes. For example, genes under any environmental circumstances whatsoever never allow an egg with the heritage of a worm to develop into a bird, nor do human genes freighted with the handicap of idiocy ever produce an intellectual leader.

5. The Rôle of Genes in Somatic Differentiation

An essential feature of cellular differentiation is the unequal division of the cell contents, both quantitatively and qualitatively. When we trace the complicated adult organism backward step by step to the fertilized egg from which it started we see that its complexity has arisen largely through this process of unequal division.

Moreover, each stage in the "process of becoming" is conditioned upon what has already happened in preceding stages, since differentiation is a forward-moving sequence of events. Just as the roof of a house must follow and not precede the erection of walls which are placed on a foundation previously prepared, so the hereditary matter in the gene must pass through a long series of preliminary steps of differentiation before finally coming to manifest fruition in the soma.

Weismann who, by the process of logic rather than experimentally, located the germinal substance in the nucleus of the germ-cell, assumed an elaborate theoretical system of "biophores," "ids," "idants," etc., whereby a differential distribution of the nuclear substance of the germ-cells to the various somatic cells is supposed to occur. This system of differentiation is diagrammatically shown in Figure 79.

Subsequent discovery and confirmation of the facts of mitosis, however, have shown that the germplasm does not influ-

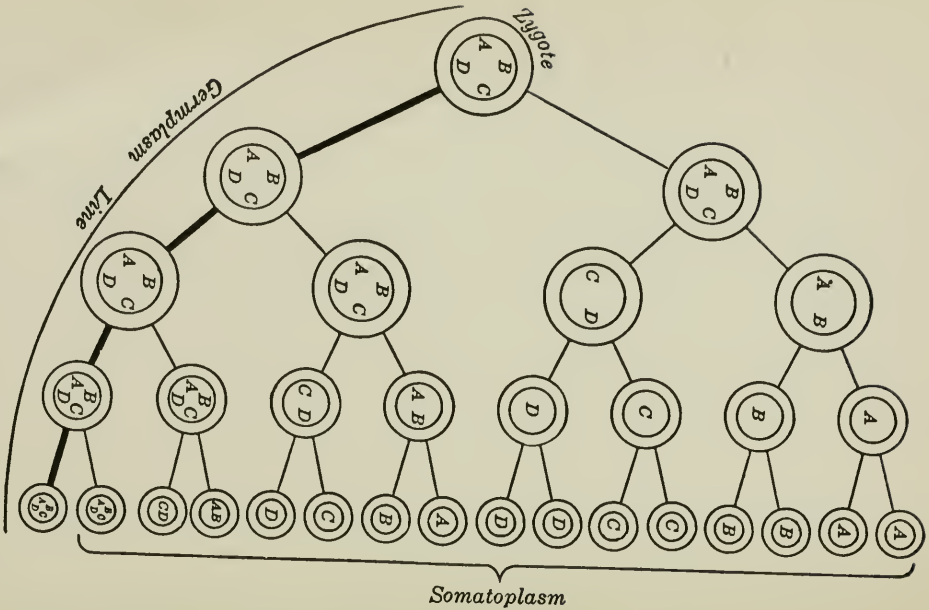

FIG. 79.—Differentiation in somatogenesis according to Weismann. Modified from Conklin. The large outside circles represent cytoplasm, the inside circles the nuclei. Differential distribution of nuclear substance.

ence development in this way, for everything indicates that the entire machinery of mitosis is directed toward securing an *equal division of the heredity-determining chromatin* for the two daughter-cells at each division. Ordinarily the entire double chromatin complex is handed down from cell-generation to cell-generation in the development of the soma regardless of the type of tissue to be formed. The question now logically follows: How can identical germinal substance give rise to different products in the formation of different kinds of cells? How can a nerve cell, for example, so depart from its generalized embryonic spherical form that its cyptoplasm becomes drawn out into enormously attenuated neurones tingling with neuro-fibrils, while a cartilage cell, with the same outfit of germinal determiners in its nucleus, and the same initial form, commits cytological suicide by the excessive secretion of its cell wall?

DeVries in his theory of "intra-cellular pangenesis" (1889) postulates, as a way out of this dilemma, *enzymatic "pangenes,"* of which each nucleus contains a complete set, that escape from the nucleus into the cytoplasm and so control its differentiation—an explanation "which nearly meets the present requirements and fits present knowledge." *It is the cytoplasm and not the nucleus that differentiates,* although the directing stimulus for differentiation comes somehow from the nucleus.

This conception of cytoplasmic differentiation directed by nuclear influence of some sort (diagrammatically shown in Figure 80), furthermore explains how the stamp of the germplasm upon the somatoplasm can determine not only immediate cell-division but all subsequent ontogenetic divisions until the adult structure results. The cytoplasm differentiates, not the nucleus.

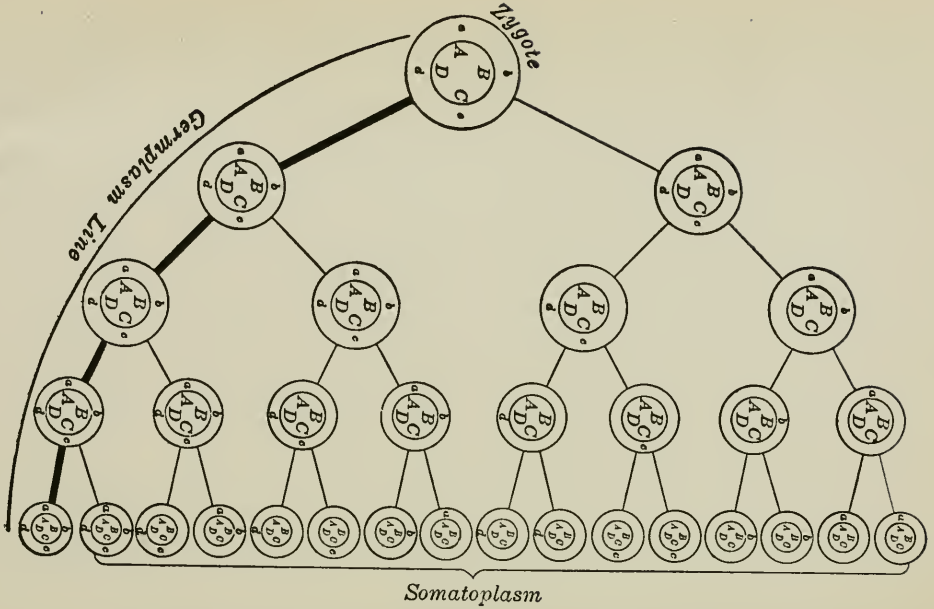

FIG. 80.—Differentiation in somatogenesis according to deVries. Modified from Conklin. The large outside circles represent cytoplasm, the inside circles the nuclei. Enzymatic pangenes migrate differentially from the genes in the nucleus into the surrounding cytoplasm and bring about its modification. The cytoplasm differentiates, not the nucleus.

6. "Cytoplasmic Inheritance"

While the germinal determiners in the chromosomes are being apportioned to the daughter-cells with strict impartiality by mitosis, the cytoplasm surrounding the nucleus does not meet the same fate. The unequal distribution of the cytoplasm, even in the early cleavage stages of somatogenesis, is quite apparent. Moreover, in the cytoplasm of the fertilized egg of many forms qualitative differences may already be detected that prophesy clearly the course which differentiation is to take.

The point of entrance into the egg of the sperm at fertilization, for example, determines the cytoplasmic region for the location of the head end of the future embryo. Thus, polarity within the fertilized egg, as well as the particular type of subsequent cleavage which is dependent upon the amount and distribution of the yolk within the egg-cell, is shown to be an extra-nuclear feature of cytoplasmic origin. When the fertilized frog's egg divides for the first time into the two-cell stage these two cells are the ancestors of the right and left sides of the animal and the cleavage plane between them marks the future long axis of the body.

The fact that so many eggs clearly show polarity and indicate the future symmetry of the organism before development has begun at all is further evidence of the important part that the cytoplasm plays in somatogenesis.

Conklin cites the ascidian *Styela* as an illuminating case demonstrating the localization of cytoplasmic determiners. In the egg of this animal the cytoplasm in different regions varies distinctively in color so that these parts may be unquestionably followed in subsequent cleavage and their fate definitely discovered.

The peripheral area of the cytoplasm of this egg containing yellow coloring matter finds its way into the cleavage cells which become muscles and mesoderm; a gray area is differentially assorted into cells that become nervous system and notochord; a slate-blue part proves to be the source of entodermal cells and a region of colorless substance gives rise to ectoderm cells.

Most egg-cells are more reticent than *Styela* in revealing the part that their cytoplasm is to play in ontogenesis, but it has been possible in many instances to trace cell-lineage through the cleavage stages until the results of differentiation are unmistakable in the tissues.

Thus while the chromosomes with their invisible genes are the ultimate determiners of heredity, the enveloping cytoplasm that surrounds the nucleus, particularly of the egg-cell, may be the immediate arbiter of the differentiation processes that characterize at least the earlier stages of somatogenesis. "In short," as Conklin says, "the egg cytoplasm determines the early development and the sperm and egg nuclei control only the later differentiations. . . . The chromosomes are chiefly concerned in heredity, the cytoplasm in development."

Correns describes a case of so-called *maternal inheritance* in *Mirabilis albomaculata* in which characters seem to be transmitted by means of something located outside the chromosomes in the cytoplasm of the egg. In this variegated four-o'clock the chlorophyll is irregularly distributed, forming blotched leaves and stems. Self-fertilized flowers from green stems give only green plants, while those from chlorophyll-less branches produce only their own kind which perish. Seeds from variegated branches produce all three kinds.

In crosses between green and non-green plants progeny is produced in which the maternal parent dominates, whichever

way the cross is made, showing transmission, unlike ordinary bi-parental inheritance, through the female line alone. Since the female germ-cell is unlike the male germ-cell principally in the amount of cytoplasm which it carries, the inference is that "maternal inheritance" in the case just described is to be explained on the basis of cytoplasmic inclusions in the ovule.

These inclusions are identified as the *plastids* of the botanist, definite structures, usually bearing chlorophyll that may be seen in the cytoplasm of the cell. Since they are present in the egg and absent from the sperm, with its minimum of cytoplasm, their transmission must be entirely through the female line.

Although the cytoplasmic plastids, like nuclear chromosomes, are self-perpetuating, always arising by fission from preëxisting structures of the same kind, yet they are not governed by an exact mitotic mechanism and consequently do not follow the usual laws of Mendelian inheritance. The renewal of cytoplasmic plastids is more like the ordinary processes of regeneration than the complicated syndesis and assortment of chromosomes. So far as is known, as Gates points out, there is no such thing as the regeneration of a chromosome.

There is nothing in what has been said of "cytoplasmic inheritance," however, to conflict with the generalization that the real determiners of heredity are germinal, for it is the genes in the nucleus of the parent germ-cell that give the character to the egg of the daughter-cell, both to its nucleus and to its cytoplasm, although the latter in turn influences somatogenesis, particularly its early stages. Apples fertilized by foreign pollen are unmodified by the contribution from the male parent because the fruit develops out of ma-

ternal tissue. In an excellent criticism of the rôle of nucleus and cytoplasm as vehicles of heredity, Dunn [1] concludes: "For development, its mechanism is but grossly known, but we have learned enough of the determinative effect of the nucleus and of the possibilities of interaction between cytoplasm and nucleus to foster a suspicion that one day the governance of the chromosomes over development will be explained in physical terms."

7. The Physical Stage-setting

During development the organism is beset on all sides by various external physical factors, which are more or less necessary to its life, and the modification of these factors brings about a corresponding variation in the normal progress of somatogenesis.

These external factors, such as temperature, moisture, light, chemical solutions, pressure, etc., may accelerate, retard or even inhibit the normal course of events, but invariably such external environmental factors contribute largely to the end result of somatogenesis.

It is quite likely that many kinds of monsters and defective organisms are the result not of defective heredity but of alterations in the normal constellation of physical factors which constitute the environment of the developing organism.

8. The Rate of Development

No doubt one essential feature in the development of an organism is differentiation or the unequal assortment of material as already mentioned in a preceding paragraph, but another factor in somatogenesis is surely the time element as it appears in the acceleration or retardation of the processes

[1] Amer. Nat., Vol. LI, 1917, p. 286.

concerned. Not all tissues or organs develop at the same rate. Some outrun others necessarily in order to prepare the way for what follows. Under normal conditions in ontogenesis things swing into place in the nick of time to make the next step possible. When these rhythms are upset, just as when Field Marshal Grouchy at Waterloo failed to swing his troops into line at the critical moment, then there results a Waterloo in the organism. To anyone who has followed in detail the intricate stages of ontogenesis in some organism, conditioned as it is by its indispensable and modifiable environmental complex, the wonder grows that the successes are so many and the disasters so few.

9. The Internal Environment

Not only is somatogenesis hedged about by external modifying factors but there is also an *internal environment* that controls to a large degree the behavior of hereditary factors and determines how they shall come to expression in the somatoplasm.

The obvious way in which growth is dependent upon the intake and use of food, and the abnormal outcome following an unnatural chemical situation within the body, such as the presence of poisons, are illustrations of what is meant by internal environment. Perhaps the best illustration of this is furnished by the endocrine glands. Twenty years ago very little was known with certainty about the part that these ductless glands, which are not confined to mammals, play in the organism, but to-day they have become so important in modern medical research that *endocrinology* is now recognized as a very lusty infant in the family of biological sciences.

The chief endocrine structures in man are the thyroids, parathyroids, the two functionally and anatomically distinct

lobes of the pituitary gland, pineal gland, adrenal glands, portions of the pancreas and the various sex glands (testes, prostate, ovaries, etc.). These structures are *physiological regulators* and have to do with the growth and development not only of the body but also of the mind. Human instincts, emotions, mental and psychic states are stimulated, inhibited, altered and complicated by endocrine action. The endocrines, therefore, constitute a large part *of the machinery through which heredity must act* to bring about its results and consequently it is possible to control, to a considerable extent, the development and behavior of man through the internal secretions produced by these glands. "Some people are born with so stable an endocrine relation," says Bandler, "that nothing will alter the normal interaction of the endocrine glands; others inherit or acquire endocrines so unstable or deficient that nothing else can elevate them to the threshold of the normal."

10. Conclusion

It is not enough for the geneticist to know the chromosomal machinery at the beginning of his story and the Mendelian moral at the end of it. Between these two fields of investigation lies the no-man's land of somatogenesis which forms an important part of the hereditary tale.

The processes of somatic differentiation are so amenable to experimental interference that no doubt future investigators will continue to be attracted to the cultivation of this promising field of genetics, which is coming to be recognized as the science of *Experimental Biology*.

CHAPTER XIII

THE DETERMINATION OF SEX

1. Prevalent Ideas

The mechanism of sex determination has been a matter of speculation since time immemorial and many erroneous as well as impossible ideas remain even to-day in the mind of the layman. These speculations fall into three categories, according to whether the belief is held (1) that the sex of the offspring is predetermined before the egg is fertilized; (2) that it is determined at the time of fertilization; or (3) that it is not determined until after the zygote has been formed.

All the older experiments on sex were based on the last of these suppositions. It was believed that by varying the nutrition of the developing embryo, or otherwise modifying in some way the external or internal environment, either sex, as desired, could be obtained. This belief was applied even to human beings, and with apparent success in many instances, since either sex is to be expected in 50 per cent of the cases, regardless of the treatment to which the developing embryo is subjected.

Experiments on tadpoles also seemed to give definite positive results in sex determination, but we now know that the death rate in some of these experiments was so large that results may be more truly explained as due to differential mortality.

Others held that the age or vigor of the parent determines the sex, the older or more vigorous of the two parents tending to impress its sex upon the offspring.

Yet another belief, and one still held by many, regards the freshness or staleness of the egg as the important factor in predetermining sex. According to this idea it is thought that an egg shortly after ovulation tends to produce a female, while one that remains some time in the oviduct before fertilization tends to produce a male.

The idea that two distinct types of eggs are formed is not altogether new. Thus, entirely without biological foundation, the theory has been propounded that one ovary gives rise to male-producing eggs and the other forms female-producing eggs. This hypothesis fails to account for the production of two sexes in birds, since usually only the left ovary persists to maturity in these animals.

Equally without foundation is the theory that in one testis male-determining sperm are produced and in the other, female-determining sperm.

Modern theories of sex determination hold to the first and second of the three possibilities mentioned above. If there are two kinds of eggs, male-producing and female-producing, then the sex of the individual is already fixed at the time of the extrusion of the first polar cell, before the sperm-nucleus has united with the egg-nucleus in fertilization. If there are two kinds of sperm, male-determining and female-determining, then sex depends upon the type of sperm uniting with the ovum, and it may, therefore, be said that sex is determined at the time of fertilization.

2. Sex Chromosomes

Our present-day stand on sex determination, which has been worked out largely upon animals rather than plants, is more scientific since it is based upon direct observation both cytological and experimental. In 1902, an *unpaired chromo-*

some was first observed by McClung in the testes of certain grasshoppers. This he called a sex-determiner. The association of this chromatic body with sex determination proved to be a discovery of primary importance. In fact it opened a new era in cytology and heralded the beginning of a large number of observations and experiments as well as much profitable discussion dealing with the mechanism of sex determination.

In many groups of animals there is an unpaired chromosome in the male, called the *x*-chromosome, which may be seen in the somatic cells, in the spermatogonia and in the spermatocytes (Fig. 81). In the female cells, both somatic and germinal, the *x*-chromosome is paired. During the process of spermatogenesis in the male the chromosomes pair to form *tetrads* in the first spermatocyte division but are later reduced to *dyads* in the second spermatocyte division, when the *x*-chromosome passes undivided to one of the second series of spermatocytes (Fig. 81), leaving the other spermatocyte of the second division accordingly with no part of the sex-determining material. During the division into spermatids the former second spermatocyte, now freighted with the *x*-chromosome, gives rise to *x*-bearing cells which form *female-determining sperm,* while the other second spermatocyte, which did not receive an *x*-chromosome, gives rise to two *male-determining sperm.*

Hence, any zygote receiving two sets of *x*-chromosomes becomes a female, while a zygote receiving only one *x*-chromosome becomes a male.

The *autosomes,* that is all the other chromosomes which have to do only indirectly with sex-determination, segregate out in the resulting gametes in normal fashion, thus securing a complete outfit of autosomal genes for each mature germ-cell. Since both types of sperm are ordinarily formed in equal

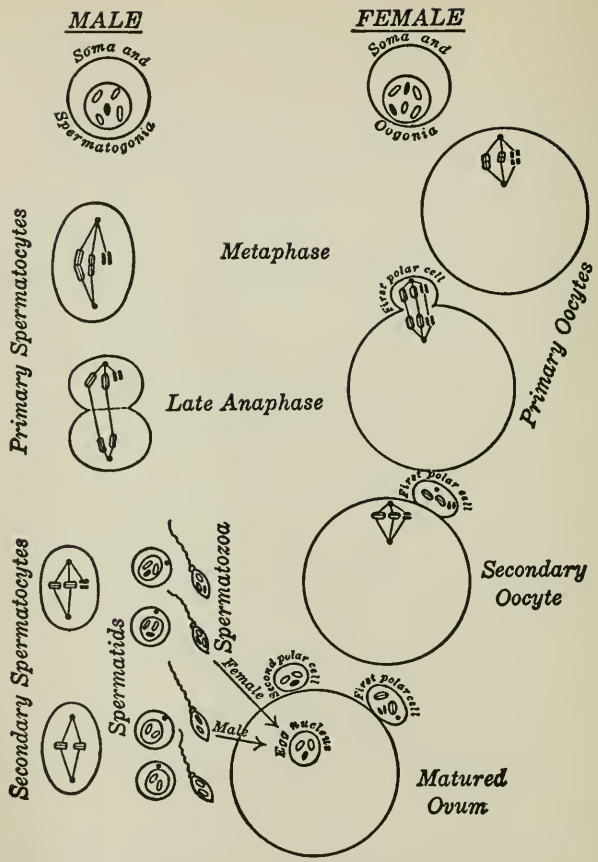

FIG. 81.—Sex determination in the case of heterogametic males.

numbers, the chances that a male- or a female-determining sperm will reach the egg in the process of fertilization are equal and the resulting zygotes, therefore, are approximately 50 per cent male and 50 per cent female (Fig. 82), which corresponds to the observed ratio of the sexes in most animal forms.

A. THE Y-CHROMOSOME

The foregoing is the simplest case of sex-determination known and, while this is the fundamental type, still there are many variations of the mechanism. For example, the *x*-

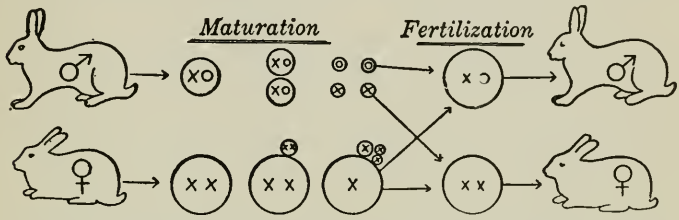

FIG. 82.—Diagram to show how numerical equality of the sexes results when one parent is homozygous (the female in this instance) and the other is heterozygous for the sex character.

chromosome, instead of being unpaired, may have a "*y*" partner in the male cells, in which case, if n = the haploid, or halved, set of autosomes in a given animal, then the following formula holds true:

$$2n + xy = \text{male and } 2n + xx = \text{female.}$$

In the spermatogonia of animals maturating in this manner, half the spermatids receive an *x*-chromosome and half a *y*-chromosome, the latter being the male-determining sperm.

In certain other cases the *x*-chromosome may be represented by several discrete, or separate, components, while it may or may not have a *y*-chromosome associated with it in the male cells. Thus, in the bug *Gelastocoris,* the male is represented by the formula $2n + (4x + y)$ and the female by $2n + 8x$. Here "n" equals fifteen, so that the male diploid number of chromosomes is thirty-five and the female, thirty-eight.

Different kinds of combinations of sex chromosomes that

have been found in different species are listed in Wilson's "The Cell in Development and Heredity." Until recently the *y*-chromosome has not been known to carry specific active genes for bodily characters. In certain fishes and in *Drosophila,* however, factors have been located in the *y*-chromosome, in which cases the characters involved are passed on only from father to son.

In general the *y*-chromosome has been regarded as merely a degenerate *x*-chromosome that has lost its sex genes and most of its other genes as well. That it is essential to the typical development of those species where it is normally present, however, has been proven in the "non-disjunction" experiments of Bridges. A male *Drosophila* without the *y*-chromosome, for instance, is sterile. These are facts of actual observation and not simply theoretical considerations.

In many forms it is not unlikely that there is no sex-determining mechanism visible even with the aid of the best microscopes, but, nevertheless, it is probable that *x*- and *y*-chromosomes exist, and that the *y*-chromosomes are practically equal to the *x*-chromosomes in size and appearance, differing from them merely in the absence of specific genes contained therein.

It may be noted that theoretically sons receive only gene-bearing *x*-chromosomes from their mothers, since the *y*-chromosome from the father is without demonstrable genes. Therefore, in the absence of any possible dominance, since there are no active allelomorphic partners provided by the *y*-chromosome, all the maternal sex-linked characters in the *x*-chromosome ought to be exhibited in the sons. The sex-linked characters of the daughters, on the other hand, since in their formation a gene-bearing *x*-chromosome is contributed by each parent, will follow the regular laws of Mendelian dominance and recession in their somatic expression, by reason of the

fact that in their formation a gene-bearing *x*-chromosome is contributed by each parent.

Thus, aside from the autosomes the son carries no paternal genes, while the daughter has a full complement of them. The daughter, on the other hand, has a full complement of genes of all kinds carried equally from both parents. These facts may account for the popular idea that sons are more likely to "take after" the mother than after the father.

B. SEX GENES

In the female, except in those cases where difference in chromosomal size is present, the *x*-chromosomes cannot always be distinguished from ordinary autosomes and it is furthermore known from breeding experiments that they bear in addition many genes for characters having nothing to do with the determination of sex.

Such characters are called *sex-linked* characters, because they always go along with the sex-determining mechanism, although they may play no direct part either in the determination of sex itself or in the formation of the "secondary sexual characters" that distinguish the sexes somatically.

That there are sometimes specific genes in the *y*-chromosome which, working in conjunction with autosomal genes are capable of producing either males, females or intermediates, in cases where the normal relationship is upset, has been indicated very clearly, especially by Bridges in recent experiments on *Drosophila*.

Sex, in other words, is now put upon a basis of specific genes, and is to be regarded as a heritable "character" as truly as any other character.

We are, therefore, entirely rid of the older idea that the *x*-chromosome is composed of a different kind of chromatin

from that found in the autosomes and that the sex of the zygote depends upon the *amount* of *x*-chromatin it receives.

c. THE METABOLIC DETERMINATION OF SEX

Riddle, basing his conclusions upon an exhaustive series of very careful experiments extending over many years, advances the idea that sex-determination is conditioned by the kind and rate, or more briefly, by the degree of metabolism, as indicated, for example, by an increase in the rate of oxidation, more water content and less protein storage, in which case there is a tendency toward male production, while with a lessened rate of metabolism, less water content and more protein storage, females are produced.

To summarize the matter in Riddle's own words, "The chromosomal constitution is not an efficient *cause* of sex; it is but a sign or index, and possibly an assistance in the *normal* maintenance of what is essential, namely, two different metabolic levels." And in somewhat more detail, "We may conceive that sexually differentiated organisms, from the first, have had the problem of producing germs pitched at two different metabolic levels; and if two sharply opposed sexes are to result from these two kinds of germs then the two metabolic levels must be measurably distinct. This task of producing and maintaining two kinds of cells pitched at two different levels ultimately falls upon *cells,* and these have, sometimes at least, produced two different chromosome complexes in connection with or in accommodation to the establishment of these two metabolic levels. But, as we have seen, the requisite metabolic level of the germ may be established in the absence of the appropriate chromosome complex, and the sex of the offspring made to correspond with the acquired grade or level of metabolism."

The adherents of the chromosome theory of the determination of sex, of course, maintain their position in the face of this evidence by assuming that the degree of metabolism is determined by the chromosomes, so that, after all, sex-determination remains primarily a matter of hereditary genes rather than of physiological response.

It may at least be said of Riddle's work upon the determination of sex that territory hitherto labeled as "impossible" has been opened for investigation.

D. HETEROGAMETIC FEMALES

The reverse of the mechanism, in which two kinds of sex-determining sperm are present, is found in the *Lepidoptera* and birds. In these groups the presence of $2n + xx$ constitutes a male and $2n + x$, a female. The formulæ in these cases are usually written $2n + zz$ and $2n + z$, in order to distinguish them from those of heterogametic males.

The cytological proof for the *z*-chromosomes is not as strong as for the *x*-chromosomes, since both avian and lepidopteran chromosomes are peculiarly difficult to study. Nevertheless, the facts are well borne out by breeding experiments in both groups.

Definite results have been reached by Seiler and also by Doncaster in experiments with moths, showing that two types of ova are produced, namely, one which, after losing the *z*-chromosome by extruding it into the polar cell and becoming fertilized, produces females, and another which, retaining the *z*-chromosome, produces males.

It is obvious that in this case (see Fig. 83), the sex of the zygote depends entirely upon the *result of maturation of the ovum,* the retention or expulsion of the *z*-chromosome being the deciding factor in the determination of sex. If in any

way maturation can be controlled by factors exerting an influence either from within the egg itself or external to it, then sex ratios may be altered from the normal 50 : 50. This has apparently been done by Seiler in the case of moths by modi-

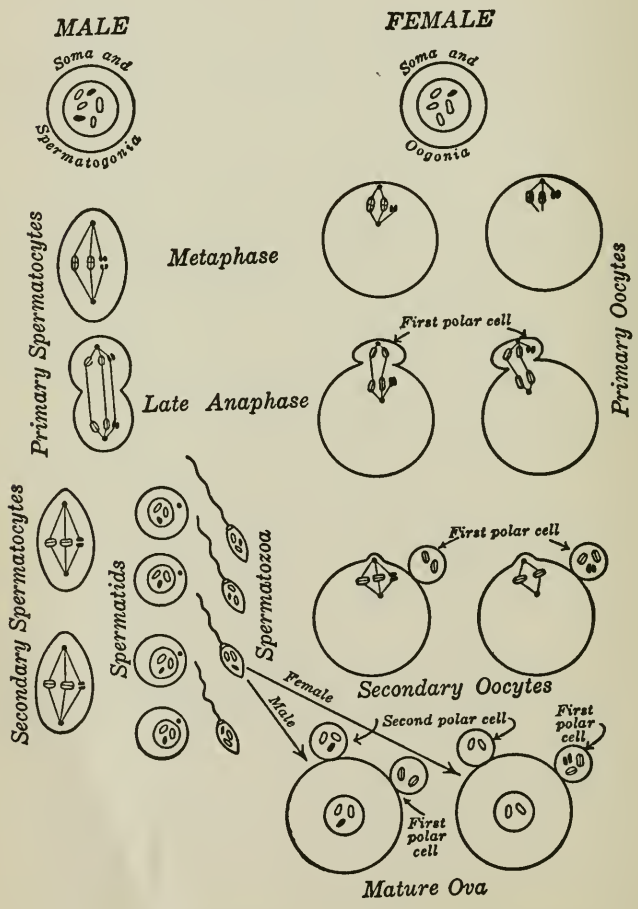

FIG. 83.—Sex determination in the case of heterogametic females.

fying the temperature of the developing ova at a critical time in the process of maturation.

The control of maturation offers a possible explanation of such sex ratios as have been obtained by Riddle in his outcrossing experiments on doves, where mostly females are produced in the latter part of a forced extended breeding season, and mostly males only in the early part of the season, instead of the usual equality of male and female.

3. Sexual Cycles

A. APHIDS AND PHYLLOXERANS

Most enlightening observations on the determination of sex by means of influencing maturation, have been made upon aphids and phylloxerans by Morgan and by von Baehr. It is well known that in the case of *Aphis* fertilized eggs always produce females. Under favorable conditions both males and females are produced parthenogenetically, the males, however, always arising from smaller eggs than the females.

It has been observed too that in these smaller eggs (Fig. 84) an entire *x*-chromosome is extruded in the giving off of the one polar cell, leaving in the egg $2n + x$ chromosomes (five in number) and that such an egg forms a male. On the other hand, in the larger parthenogenic eggs no whole *x*-chromosome is extruded into the single polar cell given off and consequently the egg, retaining $2n + xx$ chromosomes (six in number) develops into a female.

In the spermatogenesis of these forms it has been found that only one secondary spermatocyte develops from each primary spermatocyte, namely, the one which receives the *x*-chromosome. Thus, only two instead of four spermatids result from a primary spermatocyte and these two form female-determining spermatozoa. The "winter eggs" of these insects

APHID-PHYLLOXERAN CHROMOSOME CYCLE

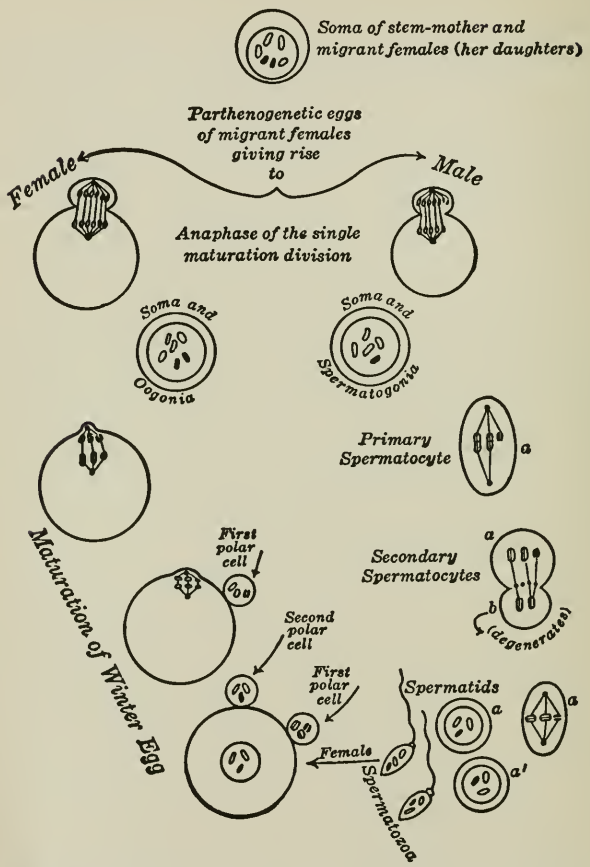

FIG. 84.—The chromosome cycle in parthenogenesis of aphids and phylloxerans.

have two maturation divisions reducing the chromosomes to the haploid condition. The female diploid number is restored upon fertilization.

It would seem, therefore, that in the phylloxerans and aphids at least, maturation is actually controlled by the size and composition of the egg.

B. ROTIFERS AND DAPHNIDS

It is unfortunate that the rotifers and daphnids, which lend themselves so favorably to breeding experiments, are not as favorable cytological material as the homopterons, for it is not at all unlikely that their sex-determination rests upon a similar basis to that above described, for aphids and phylloxerans.

In rotifers and daphnids, as in homopterons, fertilized eggs give rise to females, whereas during parthenogenesis both females and males may arise, the latter coming from smaller eggs than the former. These facts are all the more interesting for the reason that Whitney and A. F. Shull, working separately on rotifers, have been able, through modification of external conditions, to alter the normal cycle of reproduction, by causing the continuance of the parthenogenetic process beyond the normal limit.

It seems evident that, through the modification of external conditions, they have succeeded *in influencing the type of egg produced*. If this case is really parallel to that of *Aphis* and *Phylloxera,* then the type of egg artificially produced ought thereafter to control its own maturation and its sex production.

In daphnids, where parthenogenesis alternates with the sexual cycle, there are two kinds of eggs produced: (1) thick-shelled, yolk-laden, ephippial eggs which must be fertilized in order to develop; and (2) smaller, thin-shelled, parthenogenetic eggs, which develop without fertilization into females or males, depending upon environmental conditions.

The type of egg produced, as shown by Smith, Banta and

others, may be influenced by temperature and also by food and other factors. It is not improbable that we may yet discover in the maturation of these ova differences in chromosomal behavior correlated with each type of ovum and the sex of the resulting offspring.

The sexual eggs are known to be *haploid,* that is, with half or the reduced number of chromosomes, while parthenogenic eggs are *diploid,* with the double or unreduced number.

C. THE HONEY BEE

Closely allied to cases of diploid parthenogenesis in the sex cycle of the foregoing organisms, is the question of sex-determination as observed in the *Hymenoptera.*

Even before chromosomes were known, Dzierzon (1848), postulated that male bees (drones) are formed from unfertilized eggs, and females (workers and queens) from fertilized eggs, a view which has been substantiated by both cytological and genetical observations. It is known that the male honey bee has 12 chromosomes, while the female possesses the double number of 24. In this case the sex depends upon whether or not fertilization occurs. Newell has shown that in the cross between Italian (gray) queens and German (dark) drones, as well as in reciprocal crosses, the male offspring are purely maternal in color, while the females are hybrid in character. Cytological observations by Petrunkevitch and by Nachtsheim have also established the validity of the Dzierzon theory.

Coupled with this, studies on the spermatogenesis of *Hymenoptera* have revealed the fact that the spermatogonia possess solely the haploid number of chromosomes, and in order, therefore, that this number be not further reduced in the process of maturation, only one division of chromatin takes place. In the first spermatocyte division of the honey bee

all the chromosomes pass to one-half of the cell, only a minute degenerate non-chromatic globule being formed at the other pole of the spindle. In the second spermatocytic division the chromatin divides but one of the spermatids is very small and degenerates. Thus, instead of four spermatids, only one is formed and this one contains the haploid number of chromosomes.

Variations of this process are found in other *Hymenoptera* which frequently result, in the formation from the larger second spermatocyte, of two separate spermatids each possessing the haploid number of chromosomes.

4. Polyembryony

Closely allied to the chromosomal basis of sex are the facts of polyembryony, for when more individuals than one are formed from a single ovum they are invariably of the same sex. Classical examples are parasitic *Hymenoptera,* principally of the families *Proctotrypidæ* and *Chalcididæ,* in which thousands of individuals often result from a single egg. Other examples are the quadruplets formed in the nine-banded armadillo, *Tatusia,* and identical or monochorial twins in man and other mammals.

If "identicals" are due to members of a litter being developed in a common environment, then all sorts of animals that are litter mates should be of the same sex. This, as is well known, is contrary to fact and brings us back to hereditary genes either with or without the *x*-chromosome as the probable basis for the determination of sex.

In *Hymenoptera* sex depends entirely upon whether fertilization or parthenogenesis takes place. A fertilized egg will result in females and an unfertilized one in males, a supposition based upon direct cytological observation. The facts of

polyembryony thus offer strong substantiation to the idea of chromosomal determination of sex.

5. Sex-linked Inheritance

The association of Mendelian characters with particular chromosomes is nowhere better shown than in the case of sex-linked characters, the genes for which are undoubtedly located in the sex-chromosomes, and whose inheritance follows exactly the distribution of these chromosomes. Over eighty genes of this kind have been discovered in *Drosophila* alone. (Fig. 76, left-hand line.)

Sex-linked inheritance, which means that genes for characters *other than sex* are associated with a particular sex, i.e., are carried in the same chromosome that bears the sex-determining genes, should not be confused with *sex-limited* characters, i.e., with secondary sexual characters that are found in one sex only, but the genes for which may be located in any chromosome.

Sex-linked characters are not limited to either sex, as has been shown, but appear more frequently in the heterozygous sex, whichever it may be.

a. drosophila's red eyes

An example of a dominant sex-linked character is the red eye of *Drosophila*. The manner of its inheritance is as follows:

If a red-eyed female is mated with a white-eyed male (Fig. 85), the F_1 generation are all red-eyed, and when members of the F_1 generation are inbred, the F_2 generation shows the expected proportion of three red-eyed individuals to one white-eyed. However, a peculiar result appears inasmuch as all of the white-eyed individuals are males. Thus, one-half of the F_2 males are white-eyed like their grandfathers while all of

the F_1 females are red-eyed because the character of white-eyes is covered up when the gene for red is present. Those eggs of F_1 females, however, which eliminate the genes for red eyes in the polar body during maturation and are then fertilized

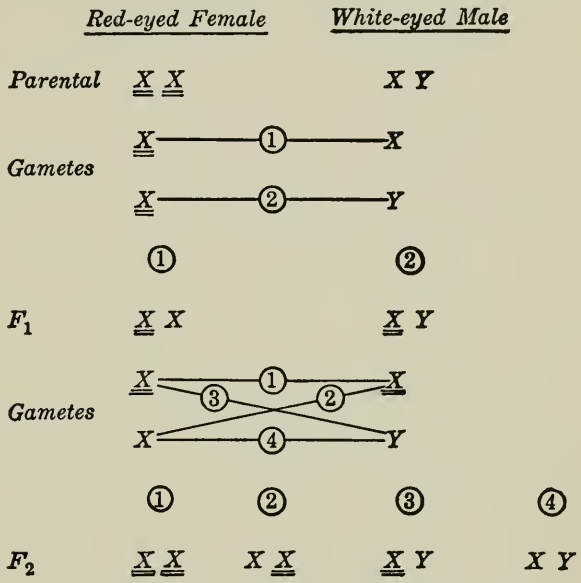

Fig. 85.—Criss-cross inheritance. The underscored *X* means the presence of the genes for red eyes in the sex-chromosome. The male is heterozygous.

by a sperm bearing a *y*-chromosome, mature into white-eyed male offspring.

The reciprocal cross of white-eyed females with red-eyed males, gives an entirely different result (Fig. 86). It will be seen that in this case the F_1 females are red-eyed like their fathers, while the males are white-eyed like their mothers. In the F_2 generation half of the males and half of the females are white-eyed and the others are red-eyed, due to the fact

that the male mechanism, which has only one *x*-chromosome, is capable of bearing the gene for red in only half of its germ-cells. The F_1 females, all of which normally carry two *x*-chromosomes, all receive an *x*-chromosome from their father and are consequently red-eyed, while the F_1 males all receive

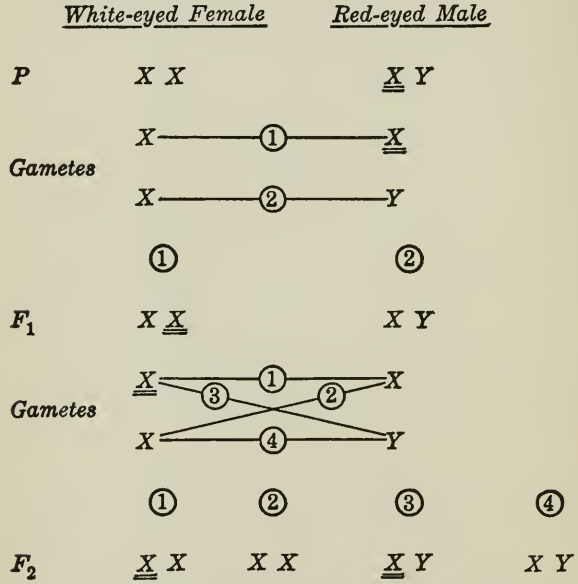

FIG. 86.—Criss-cross inheritance. The reciprocal cross to that shown in Figure 85. All individuals with underscored *X* have red eyes. The male is heterozygous.

a single *x*-chromosome from their white-eyed mother and are, therefore, themselves white-eyed.

These results of the crosses of red-eyed and white-eyed flies are all explainable when it is remembered that white eye color and red eye color are allelomorphic genes, located in the *x*-chromosome, and that the *y*-chromosome carries no effective genes.

B. COLOR-BLINDNESS IN MAN

This criss-cross type of inheritance has long been known in man. Color-blindness, or the inability to distinguish red and green, is perhaps the best known example of a sex-linked character, behaving in its inheritance exactly as that of red-

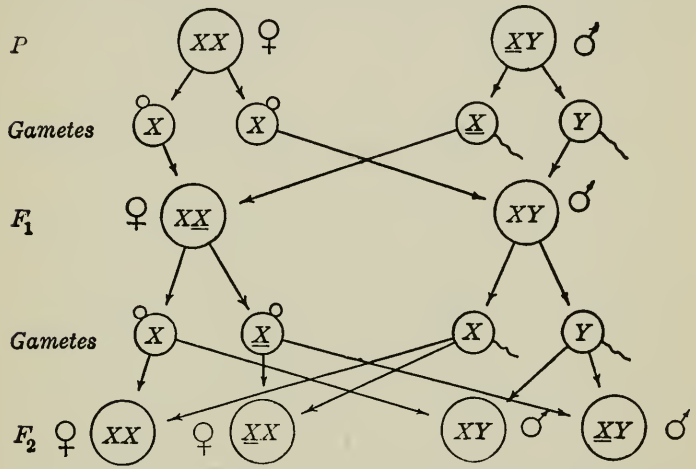

FIG. 87.—General diagram for sex-linked inheritance. The underscored symbol (X̲) represents a sex determiner with some other character (as color-blindness) linked with it.

eye in *Drosophila*. That color-blind females are so rare is due to the fact that it requires a duplex, or homozygous, dose of the determiner for color-blindness to produce a color-blind female, while only a simplex, or heterozygous, dose is needed to produce a color-blind male. These facts agree perfectly with the idea that the female is homozygous and the male heterozygous with respect to sex, and that the factor for color-blindness is linked with the determiner for sex. Sex-linked inheritance, as shown in this case, may be illustrated by the

diagram on the preceding page (Fig. 87) in which, for the sake of simplicity, only sex chromosomes and the determiners for color-blindness are represented. Underscored $\underline{X}$ represents a color-blind determiner linked to a sex chromosome.

From this diagram, which agrees substantially with the observed facts, it is apparent that a color-blind male mated to a normal female will produce no color-blind offspring, although the females will be "carriers" of color-blindness, that is, will

Parents		Expected Offspring	
♂ Normal	♀ Color-blind	♂ Color-blind	♀ Carrier
Normal	Carrier	½ color-blind ½ normal	½ carrier ½ normal
Color-blind	Normal	Normal	Carrier
Color-blind	Color-blind	Color-blind	Color-blind
Color-blind	Carrier	½ color-blind ½ normal	½ color-blind ½ carrier

possess the factor in simplex form and will, therefore, carry it *for the female* in a latent condition.

The sons of such a mating having a normal mother and a color-blind father will be absolutely free from the defect and cannot produce color-blindness in any of their offspring when mated with a normal strain. If, however, the "carrier" daughters from such a parentage, who are genotypically heterozygous for color-blindness but phenotypically normal, mate with normal individuals, the expectation is that one-half of the sons, and none of the daughters will be color-blind, but that one-half of these daughters will carry the color-blind determiner in simplex form, that is, in a condition ineffective for producing color-blindness in female individuals.

All of the various possibilities in the inheritance of color-blindness according to the sex-linked interpretation are indicated in the table on page 276.

C. THE BARRED PLYMOUTH ROCK

In animals in which the female is heterogametic (*Lepidoptera* and birds) sex-linked characters are likewise known to

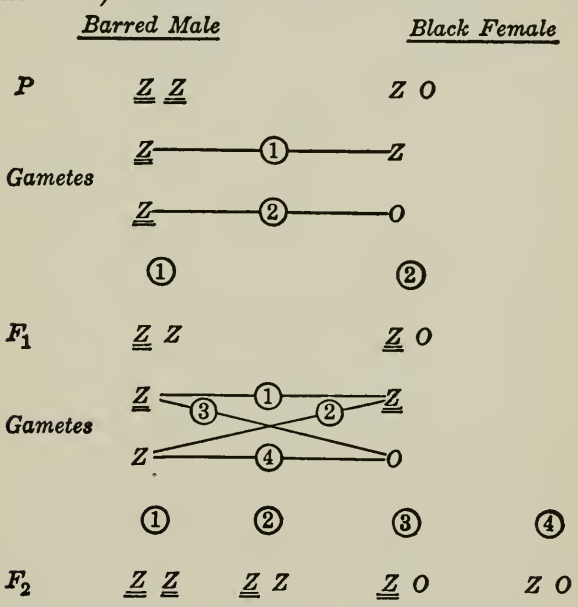

FIG. 88.—Sex-linked inheritance, with the female heterozygous. The "barred" character is indicated by underscored letters.

exist and, in fact, were first discovered in moths by Doncaster in 1908. The female instead of the male in these cases possesses the mechanism whereby the character in question can be present only once.

For example, "barring" is a dominant sex-linked trait in poultry, as shown in Figures 88 and 89.

In the cross shown in Figure 88 all the males and half the females in the F_2 generation are barred while in the reciprocal cross shown in Figure 89 the F_1 males are barred because they have a *z*-chromosome from their maternal side,

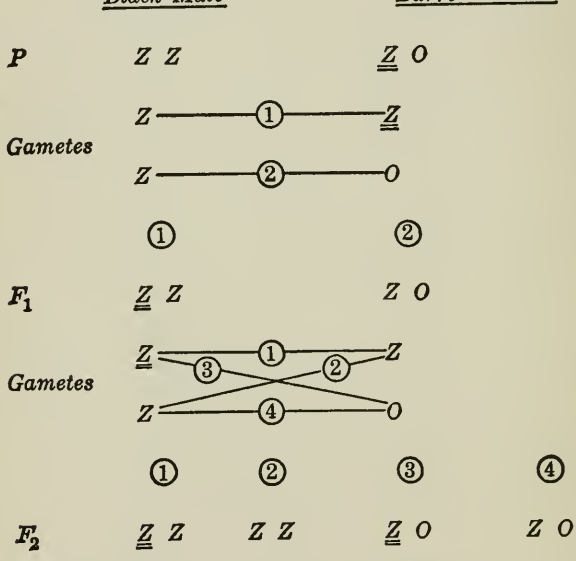

FIG. 89.—Sex-linked inheritance, with the female heterozygous. Reciprocal cross to that shown in Figure 88. The "barred" character is indicated by the underscored gametes.

while the F_1 females are black because their single *z*-chromosomes came with their black father.

By means of a white head-spot that goes along with the barring factor even in newly hatched chicks it is possible to tell the sex of the chicks directly upon hatching. For example, among the offspring of a black cock and a barred hen, as shown in Figure 89, it is known at once that all with the white head-spot will grow up into barred hens, while those

without the white head-spot will become black (unbarred) cocks.

This sex-linked factor, therefore, is of practical importance to poultrymen who wish to maintain a uniform flock.

6. Non-disjunction

A striking confirmation of the chromosomal interpretation of sex is furnished by the phenomenon of *non-disjunction* discovered in 1913 by Bridges. In attempting to explain certain unexpected ratios which he obtained in a long series of breeding experiments upon white-eyed *Drosophilas,* Bridges found that his results would be more intelligible if what he termed "non-disjunction" was assumed to occur.

By non-disjunction is meant that both the *x*-chromosomes, instead of disjoining and going normally to the two poles during the last maturation division, remain attached to each other and pass together to one pole, leaving the other pole without any *x*-chromosome. In consequence, half the mature eggs should be provided with two *x*-chromosomes and the other half with none at all. Cytological examination of these unusual flies showed that this was actually what did take place.

The cause of non-disjunction is not known, although Mavor, by exposing *Drosophilas* to x-rays, succeeded in inducing some cases of this abnormality.

The progeny of non-disjunctional white-eyed females, as shown in Figure 90 taken from Sharp's "Introduction to Cytology," show a theoretical diversity of characters which is borne out in the results of actual breeding. Morgan sums the matter up when he says: "An abnormal distribution of sex-chromosomes goes hand in hand with an abnormal distribution of all sex-linked factors."

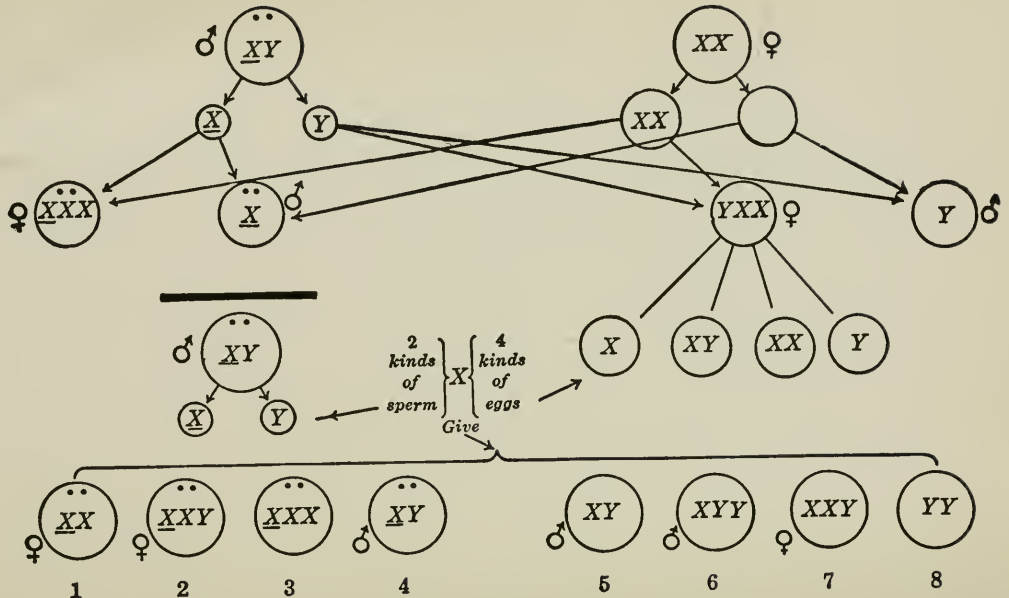

FIG. 90.—(For explanation see page 281).

Explanation to Figure 90

"Non-disjunction and its results in *Drosophila*. The two large circles in the first row represent male and female flies producing sperms and eggs respectively. Non-disjunction in the female gives 2 kinds of eggs, with *XX*- and no sex-chromosomes, instead of the normal single kind with one *X*. At fertilization there are possible 4 combinations rather than 2, as shown in the large circles of the second row. Owing to the several ways in which her 3 sex-chromosomes may be distributed at maturation, the female represented by the third circle produces 4 kinds of eggs. When mated to a normal male (below the horizontal line) with two kinds of sperms, 8 combinations are possible (last row). Numbers 1, 4 and 5 are normal flies and give the usual type of progeny. Numbers 2, 6 and 7, owing to the presence of 3 sex-chromosomes, give exceptional results when bred. Types represented by Numbers 3 and 8 do not appear in the cultures, probably because they die very early. The original male has red eyes and the original female white eyes. Red eyes (represented by the dots) appear in every fly bearing the *x*-chromosome of the original male."

(Diagram by Sharp based on data from Bridges and Morgan.)

7. Secondary Sexual Characters and Hormones

It will be seen from the preceding illustrations that the primary differences between the sexes is in the kind of gametes which they form. The female is an egg-producer, the male a sperm-producer. In many animals, especially invertebrates, it is very difficult to distinguish males from females without first examining the gonads, although there is no lack of higher forms in which one can with ease distinguish the sexes solely by external appearances.

Very often this sexual dimorphism is confined, first, to the genitalia or to accessory apparatus used in copulation, oviposition, or rearing of the young; and second, to extra-genital features not associated directly with reproduction, such as color, ornamentation, and the like. Both of these types of sexual dimorphism are, however, secondary to gamete production.

In mammals and birds these so-called secondary sexual

characters are found to be largely dependent for their proper development upon the normal presence and activity of the gonads. For example, castration of young male mammals results in individuals lacking in many ways the attributes of normal males. Among cattle and horses, which have undergone this operation, the fiery males become docile and lack the thick neck and type of body-build common to their kind. They also put on fat more readily, and exhibit a lower level in all their metabolic processes. In man the voice fails to change, the beard is sparse, the epiphyses of the bones do not fuse as completely and the spirit is dulled. Females deprived of ovaries early in life fail to develop normal mammary glands, while certain of their skeletal characters are likewise much altered. Extensive experiments have proved that in birds and mammals at least secretions of the gonads, known as *hormones,* are essential to normal development. The castration of young male rats followed by ingrafting of ovaries causes these individuals to become feminized in character.

Perhaps no better case of the influence of hormones is known than that of the "free martin," concerning which Lord Lister many years ago in a letter to Rev. Dr. Worthington [1] commented as follows:

"Pray do not part with your *free martin.* It will be a beautiful animal, docile and useful in your fields as an ox. I have dissected many, but why this mingling of the sexes should arise under such circumstances eludes all my guesses. Some of the tricks going forward in the inhabitants of the uterus I have long since pretty well made out but this is too much for me. I was the first who made the fact known (some 30 years ago) to Mr. John Hunter. He soon went to work on the subject and the result was an excellent paper in the Phil.

[1] Baron's *Life of Jenner,* p. 409.

Trans. It was republished in his work on the Animal Economy."

It remained, however, for Lillie to follow up the story of the free martin and to furnish an adequate explanation for it.

He found in cattle that when the chorionic coverings of twin embryos of opposite sex fuse so that the blood vessels anastomose, the more rapidly developing male embryo sends out hormones into the circulation which inhibit the normal development of the female embryo. The much modified female embryo may then be born as a *free martin* in which the ovaries tend to form tubules quite like those of a testis and which never produce mature ova.

In birds the activities of the gonads likewise control to a large extent the development of the secondary sexual characters, as has well been shown by Goodale and by Morgan in castration and transplantation experiments on ducks and fowls. Most striking is the case of female birds which, when castrated while still young, develop male plumage and posture.

It has been clearly demonstrated that the genes for secondary sexual characters lie in the autosomes and thus both male and female have determiners for the secondary sexual characters of both sexes. For example, normally in cases where the male is heterogametic, the presence of a single *x*-chromosome in all of its cells, together with the endocrine secretion of its gonads, causes the male genes for secondary sexual characters to develop and those of the female to be suppressed. By castration and transplantation the normal condition may be upset and the female secondary sex genes brought into action.

The whole problem of sex-hormones is very complicated since it has been shown that the secretion from the gonads is merely one link in the chain of endocrine factors that tend to set into action the genes for determining secondary sexual

characters. That is, it is not the gonadal hormones alone that are effectual in the development of secondary sexual characters, but the interaction also of the pituitary, adrenal and thyroid glands, and possibly other members of the endocrine chain, that take part in determining the result. In the development of sex in the vertebrates the genes for the production of these sex-hormones are second in importance only to those genes which determine whether ova or sperm shall be formed in an individual.

8. The Effect of Parasitism on Sex

It has been well demonstrated in insects that castration, even of very young individuals, produces no effect upon the secondary sexual characters when the animal reaches its adult form. Even the implantation of gonads of the opposite sex results in no change. The growth and development of the soma seems to be fixed by the chromosomal complex and does not appear to be influenced by the action of any sex-hormones. Alterations of secondary sexual characters may occur, however, by means of parasitism, as shown by experiments both on crustacea and on insects.

Among crustacea a classical case of this kind is that of the crab *Inachus,* the male of which when parasitized by the cirriped *Sacculina,* as described by Geoffrey Smith (1906), becomes similar to the normal female in the form of its claw, abdomen and abdominal appendages.

Among insects *Thelia bimaculata,* described by Kornhauser (1916 and 1919), is a good example. Males parasitized by another insect, *Aphelopus,* resemble females even to the minute structure of their chitinous integument. Parasitized females are not affected. Such alterations are due, very likely, to an entire upset in the metabolism of the host, changing the in-

ternal environment so fundamentally that the genes for the male secondary sexual characters fail to find the conditions necessary for their expression in the developing soma.

9. Gynandromorphs and Sex Intergrades

In insects and crustacea abnormal individuals occasionally appear, presenting both male and female characters. Sometimes the demarcation is exactly median, one-half being male

Fig. 91.—"A gynandromorph mutillid wasp, *Pseudomethoca canadensis*, male on right side, female on left." From Morgan's "Heredity and Sex," by permission of the Columbia University Press.

and the other female. Such forms are true *gynandromorphs.* (Fig. 91.) There are cases, however, where the division may be either dorso-ventral or antero-posterior, and still others which show a patchwork of male and female parts, these latter being mosaic or inter-sex individuals. Examples of such sex-intergrades have been found among moths as described by Goldschmidt and by Banta among daphnids.

Insect gynandromorphs, of which over a thousand instances have been recorded (Morgan), do not necessarily have the gonad of the corresponding sex in their respective halves,

showing that the soma is not always molded by sex-hormones.

The cause of gynandromorphism has been studied among others by Boveri and by Morgan. Boveri claims to have found in gynandromorph bees of crossed races that the male half was maternal, and the female half hybrid. Obviously, if after the division of the egg-nucleus, a sperm unites with *one* of the daughter nuclei that half will be female, whereas the sister nucleus, developing parthenogenetically, will form a male half purely maternal in origin.

This explanation certainly holds good for some cases but Morgan finds in *Drosophila* that male portions of gynandromorphs often bear paternal characters, genes of which are in chromosomes other than the *x*-chromosome. He concludes, therefore, that at times an *x*-chromosome is lost during the meiosis of a female zygote, leaving a nucleus that fails to get two *x*-chromosomes, which, consequently, develops into the male portion of the gynandromorph.

Similarly a misplaced *x*-chromosome in a primary germ-cell may cause the formation of testes in a female. Such a case of gynandromorphism in *Thelia* proved upon actual chromosome count to have one *x*-chromosome missing (Kornhauser).

It is rather difficult to offer any simple mechanical explanation for the mosaics or sex-intergrades of moths and daphnids. Goldschmidt has attempted to explain his results upon a quantitative basis, assigning values for the determiners for maleness and femaleness, and adding the assumption that the strength of these determiners varies in different races. Thus, the crossing of a strong male race with a weak male race brings about an upset of normal conditions, establishing a new balance of factors so that neither one sex nor the other

predominates. An expression of two sets of genes, therefore, is brought about in various parts of the organism.

Bridges' recent work on triploid races of *Drosophila* seems to indicate that when the normal relation of the autosomal genes to the sex-genes of the *x*-chromosome is upset, either by the preponderance of one or the other, then sex abnormalities of many sorts may be expected. Therefore, it can be definitely stated that autosomes may take indirect part in sex-determination.

10. Hermaphroditism

One of the most obscure problems of the entire sex question is that of hermaphroditism, or the production of ova and sperm by a single individual. Instances of this condition are found normally occurring in many groups of invertebrates, such as cœlenterates, ctenophores, flat-worms, round-worms, annelids, molluscs, crustaceans and ascidians. It is, however, the exception rather than the rule, although common enough in plants, and may be viewed as a modification of the bisexual condition necessitated to insure insemination in organisms poorly adapted to bring about typical fertilization.

Sometimes hermaphrodites are female in appearance and again they resemble more closely the males of the group to which they belong. In certain nematodes, for example, *Rhabdites aberrans,* an occasional male is found among thousands of hermaphrodites of female appearance. In this worm Miss Krueger has shown that occasionally there is a failure of one chromosome to become incorporated in one of the second spermatocytes. Spermatozoa resulting from such deficient spermatocytes may be the cause of these occasional male zygotes. Since our knowledge of the chromosomes in hermaphroditism is deficient, it is hardly worth while at present

to speculate on the mechanism which produces such individuals.

Angiostomum (*Rhabditis*) *nigrovenosum* is another nematode worm with an alternating hermaphroditic generation living in the lungs of frogs, which resembles the female in general appearance but whose gonads produce first eggs and later sperm.

Both Boveri (1911) and Schleip (1911) found that the hermaphroditic eggs of these animals are fertilized by sperm from the same individual. When the eggs mature the normal number of 12 chromosomes becomes reduced to 6 but two kinds of sperm are produced, one with 6 and one with 5 chromosomes, because one of the 12 chromosomes from the sex pair fails to migrate to the daughter nucleus and degenerates. When these two kinds of sperm fertilize eggs, two sorts result, eggs with 12 and eggs with 11 chromosomes. This is the composition of the alternating bi-sexual generation.

The hermaphrodites with 12 chromosomes resemble the females of the bi-sexual generation. There are no 11-chromosome hermaphrodites because either the sperm with 5 chromosomes is non-functional or the 11-chromosomes hermaphroditic zygote is lethal.

That the sexual tendencies of hermaphroditic forms are often in a sensitive balance, influenced by external conditions, is shown by the experiments of Baltzer on *Bonellia* and by Gould on *Crepidula*.

In the marine worm *Bonellia* there are produced minute motile larvæ with hermaphroditic possibilities. If these free-swimming larvæ find the proboscis of a female *Bonellia* they attach themselves thereto and develop into minute males after a parasitic existence of about four days. If, however, no proboscis is encountered, the motile larva sinks eventually to

the bottom and develops into a female. In this case we may imagine that some secretion from the female stimulates the development of the male potentialities and suppresses those that lead to the formation of the female. In fact, intermediates were produced by Baltzer by allowing larvæ to become attached to a proboscis temporarily and then removing them at intervals of less than four days.

Crepidula plana is an hermaphroditic gasteropod which is normally protandric, that is, producing first sperm and afterward ova. Gould has shown that the presence of older individuals in the female phase of development causes the production of sperm in such young individuals as, when isolated, omit sperm production, causing them instead to develop the female phase and to produce ova. Here is an animal in a sensitive balance which is presumably influenced by a secretion that probably comes to it through the sea-water from individuals in the female phase of reproduction.

The problem of hermaphroditism, its mechanism and relationship to bi-sexual reproduction, is well worth intensive study. From such exceptions to the general rule we may hope to learn much about the normal mechanism of sex-determination.

11. Sex Reversal

Contrasted with normally hermaphroditic animals there may appear, particularly under certain closely observed control conditions, abnormal organisms which exhibit various degrees of intersexuality. In such organisms, that in ordinary conditions would be either male or female, the abnormalities may be due either to some sort of disharmony in the genetic make-up of the individual, or to some unusual alteration in the activity of the sex-modifying hormones of the organism during impressionable stages of its development.

The free martin, already mentioned, is a good illustration of the modifying influence of sex hormones which when acting early in the cycle of development bring about modifications of the secondary sexual characteristics finally assumed. *Bonellia* and *Crepidula* are likewise cases of a modified sex apparently resulting from the presence or absence of a chemical stimulus emanating from a nearby sexually mature female individual.

Whenever intersexuality goes so far as to swing what was genetically one sex over to the opposite extreme of the other sex, then "sex reversal" results. This may be regarded as a sort of potential hermaphroditism induced in a form normally uni-sexual.

The farther the differentiation of distinctively phenotypic sexual characters has proceeded, the more difficult it becomes to bring about a reversal of sex, yet there appears to be evidence that such a reversal has been effected in at least a few well authenticated instances even in adult animals.

Thus Riddle cites three cases of apparent adult sex reversal. The first is that of the Alpine newt, *Triton,* reported by Champy (1921), which after having demonstrated its maleness by successfully fertilizing the eggs of a female newt, was found upon autopsy, following a prolonged period of fasting, to be filled with immature eggs and to be entirely devoid of any sperm-producing tissue.

The second case is that of Crew's famous crowing hen (1923) which, after having repeatedly produced viable eggs that were brooded and hatched, assumed not only the secondary phenotypic characteristics of a cock, but, upon being mated with a normal hen, became the father of two birds, a male and a female, which in turn were subsequently the parents of normal chickens.

The third instance is one of Riddle's doves (1924) which, after having laid normal eggs during a period of years, took on pronounced male appearance and behavior. Autopsies of both Crew's hen and Riddle's dove revealed the fact that the left ovary (the only one an adult bird normally possesses) had been entirely destroyed by tuberculosis and that testicular tissue had developed in its place.

Domm has produced sex-reversal artificially in poultry. By removing the left ovary, the aborted right ovary becomes a testis that produces viable sperm. Ponse has also induced sex-reversal in toads. When the testes are removed, Bidder's organ, which may be regarded as a rudimentary ovary, becomes functional and produces eggs.

In animals as highly elaborated as mammals it is probably useless to expect sex-reversal to occur after complete differentiation has once taken place. The same generalized embryonic structure cannot develop in turn into two different sets of reproductive organs. If differentiation has already proceeded along one of the paths that leads to the expression of one sex, it is too late for dedifferentiation to occur, that is, to go back and to follow out the alternative path that leads to the other sex.

The outcome seems to be inevitable, however, that in some cases, at least, the reproductive functioning of an individual is not irrevocably fixed by its chromosomal composition, but that the internal environment, represented by hormones of various kinds, may upset the balance and swing a genotypic male over into a phenotypic female or *vice versa.*

12. Conclusion

Finally, one may ask, can sex ever become controlled? If chromosomes are the determining factors, and there is much

evidence that they play at least the major part, then in those forms in which the male is heterogametic for sex it would be possible to produce at will either desired sex only by some agency that would differentially aid or inhibit the union of one of the two kinds of sperm with the egg. It is at present very difficult to conceive any way that this sorting out of the sperm could be practically effected. In animals like *Lepidoptera* and birds in which the female is heterogametic and forms two kinds of eggs (male-producing and female-producing) the possibility of selecting one or the other of the two kinds of eggs for fertilization to the exclusion of the other kind is equally hopeless.

"The conclusion that genetic factors are involved in the determination of sex does not in the least imply that environmental factors cannot modify the sex ratio. On the contrary there is abundant evidence that they can do so" (Hogben and Winton). If a genotypically predetermined sex may under certain conditions be reversed by overwhelming or outclassing the effect of the genetic composition through manipulating environmental factors, either external or internal, then since these factors are more or less amenable to experimental control, sex determination may not after all be entirely beyond the grasp of the experimenter.

CHAPTER XIV

THE APPLICATION TO MAN

1. The Application of Genetics to Man

The genetics of man, which awaits consideration in the following chapters, forms the new science of *eugenics*. This is a rather hazardous territory to invade because the personal human interest involved is so great that prejudice and desire are apt to influence dispassionate scientific analysis and judgment. The subject falls largely in the field of *sociology* so that the biologist is under the necessity of utilizing a new and strange vocabulary as well as of adopting different and more or less unfamiliar methods of procedure. The sociologist, on the other hand, is sometimes equally at a loss in this "no-man's land" of eugenics when he fails to evaluate properly the genetic foundations and resorts to uncertain aërial tactics.

It has seemed wise, therefore, in the present volume to preface the rather brief but highly important consideration of human heredity with the lengthy introduction of general genetic principles which makes up the bulk of the book. After all it must be remembered that eugenics is really a sort of a sociological duckling that has been hatched by a biological hen, which fact partially accounts for its rather problematical development and standing among the sciences.

Human civilization goes hand in hand with the degree of successful interference which man exerts upon the natural forces surrounding him.

Primitive man was overwhelmed and outmastered by his environment, but civilized man harnesses nature to do his will. Savages are not proficient in the arts of cultivating plants and domesticating animals, while these are the very things upon which human progress fundamentally depends. The degree of civilization of any people is closely correlated with the degree of their success in exercising a conquering control over plants and animals. Any knowledge of the laws of heredity, therefore, as applied by man, either directly to himself or indirectly to animals and plants, is a distinct contribution to human progress.

In 1900 the National Association of British and Irish Millers, as Kellicott points out, being dissatisfied with the quality and quantity of the annual wheat yield, engaged Professor Biffen of Cambridge to apply his knowledge of heredity to the practical problem of improving their wheat crop. The characters desired were a short full head, beardlessness, high gluten content, immunity to rust, strong supporting straw, and a large yield per acre. In the short time that has elapsed, Professor Biffen has succeeded in producing strains of wheat that combine all these desirable characters to a remarkable degree. Such an immediate result would not in any event have been possible before 1900, when the rediscovery of Mendel's laws revolutionized man's knowledge of the action of heredity in nature.

This same knowledge which has made possible the improvement of wheat may be applied with certain reservations to the breeding of man. Typical Mendelian ratios have not been worked out in man because that would involve the mating of brother and sister.

There is no reasonable doubt, however, that man belongs in the same evolutionary series with all other animals, as

Darwin showed, and is consequently subject to a considerable degree to the same natural laws.

It must be admitted that thus far in the progress of civilization more attention has been directed to the scientific breeding of animals and plants, little as that has been, than to the scientific breeding of man.

Carruth states the unpleasant truth that "The only extensive positive impulses to breeding given under civilization have been the breeding of negroes and hybrids for slaves, the breeding of women for concubines in oriental countries, and the subsidizing and breeding of men for cannon food in various great imperial countries."

It is to be hoped that the future will have a better story to tell.

2. Modifying Factors in the Case of Man

There are certain qualifying factors that make the problems of genetics somewhat different in the case of man than in other organisms.

For example, mankind has come to be partially exempt from some of the natural laws which affect other organisms. Thus, with respect to the workings of *natural selection,* man is partially under "grace" rather than "law." Nature no longer "selects" good eyes in man by long, patient, and devious processes of the elimination of the unfit, since poor eyes are almost always made good at once by a visit to the oculist. She has long since given up providing natural weapons of defense for those who have the wits to supply themselves more efficiently with artificial means of self-preservation, and she no longer attempts to improve the natural powers of locomotion of those who are able to tame a horse to ride upon, or who build steamships, railroads, automobiles and aeroplanes, thus accom-

plishing without delay what would require ages, to say the least, to evolve, if indeed it could ever come about by natural agencies.

Neither does the law of the *survival of the fittest* in its original sense apply equally to man and to other organisms. Human society to-day protects its unfit in hospitals, asylums, and through various philanthropies, while physicians devote themselves to the art of prolonging life beyond the period of usefulness.

We do not desire these particular consequences of our modern civilization to be otherwise, but the fact remains that some of the most inflexible and universal "natural laws" are ineffective in the case of man, and it is profitable to bear this in mind when attempting to apply the laws of genetics to man.

The laboratory for human heredity is the wide world, and it is obvious that the experimental method which has proven so effective in studying the heredity of animals and plants is impracticable in the case of man. The direct application of stock-breeder methods to man is naturally revolting to us and is not anywhere advocated, even by the most extreme of eugenists, in spite of popular opinion to the contrary.

The consideration of human heredity, therefore, must always be largely from the statistical side, consisting in an analysis of experiments already performed rather than in arbitrarily initiating new experiments. Such institutions as insane asylums, prisons, sanitariums, and homes for the unfortunate are excellent foci for studying certain phases of human heredity, simply because they are convenient places where the results of similar dysgenic characteristics have been brought together and made more easily observable.

3. Experiments in Human Heredity

a. the jukes

A classic example of an unpremeditated experiment in human heredity which has been partially analyzed by the statistical method is that furnished by Dugdale in 1877 in the case of "Max Jukes" and his descendants. At that time it included over one thousand individuals, the origin of all of whom has been traced back to a shiftless, illiterate, and intemperate backwoodsman who started his experiment in heredity in western New York when it was yet an unsettled wilderness.

In 1877 the histories of 540 of this man's progeny were known, and that of most of the others was partly known. About one-third of this degenerate strain died in infancy, 310 individuals were paupers who all together spent a total of 2300 years in almshouses, while 440 were physical wrecks. In addition to this, over one-half of the female descendants were prostitutes, and 130 individuals were convicted criminals, including 7 murderers. Not one of the entire family had a common school education, although the children of other families in the same region found a way to educational advantages. Only 20 individuals learned a trade and 10 of these did so in state's prison.

It is estimated that up to 1877 this unfortunate experiment in human breeding had cost the state of New York over a million and a quarter dollars, not including the drink bill, and the end is by no means yet in sight.

The discovery in 1911 of Dugdale's original manuscript giving the real names and localities of the members of the "Jukes" clan made it possible to follow up the later history of this famous strain of undesirable human germplasm. This was

done by Dr. A. H. Esterbrook, who published the results of his investigations under the title of "The Jukes in 1915," [1] after personally visiting every individual he could trace.

Since Dugdale's time the "Jukes," now in the eighth generation, have been forced to disperse from their original habitat because the cement mining industry upon which most of them formerly depended for a livelihood had been abandoned with the introduction of Portland cement. Esterbrook has recorded 2094 individuals bearing Jukes' blood who were scattered through fourteen states. Of 748 living descendants of Max Jukes over 15 years of age, he found 76 who were socially adequate; 255 doing fairly well; 323 "typical degenerates," and 94 whom he left unclassified due to lack of sufficient information. He says: "The removal of Jukes from their original habitat to new regions is beneficial to the stock *itself*, as better social pressure is brought to bear on them and there is a chance for mating into better families," but Davenport, commenting on the entire matter, adds: "The most important conclusion that may be drawn from Dr. Esterbrook's prolonged study of the Jukes forty years later is that not merely institutional care nor better environment will cause good social reactions in persons who are feeble-minded or feebly inhibited, although on the other hand, better stimuli will secure better reactions from weak stock than will poor stimuli. . . . The chief value of a detailed study of this sort lies in this: that it demonstrates again the importance of the factor of heredity."

B. THE DESCENDANTS OF JONATHAN EDWARDS

In striking contrast to the case of Max Jukes is that of Jonathan Edwards, the eminent divine, whose famous prog-

[1] Carnegie Institution of Washington, Pub. 240, 1916, 85 pp.

eny Winship describes as follows: "1394 of his descendants were identified in 1900, of whom 295 were college graduates; 13 presidents of our greatest colleges, besides many principals of other important educational institutions; 60 physicians, many of whom were eminent; 100 and more clergymen, missionaries, or theological professors; 75 were officers in the army and navy; 60 were prominent authors and writers, by whom 135 books of merit were written and published and 18 important periodicals edited; 33 American states and several foreign countries and 92 American cities and many foreign cities have profited by the beneficent influence of their eminent activity; 100 and more were lawyers, of whom one was our most eminent professor of law; 30 were judges; 80 held public office, of whom one was vice-president of the United States; 3 were United States senators; several were governors, members of Congress, framers of state constitutions, mayors of cities, and ministers of foreign courts; one was president of the Pacific Mail Steamship Company; 15 railroads, many banks, insurance companies, and large industrial enterprises have been indebted to their management.

"Almost if not every department of social progress and of public weal has felt the impulse of this healthy, long-lived family. It is not known that any one of them was ever convicted of crime."

Similarly Galton, in "Hereditary Genius," points out in his analysis of one hundred celebrated persons that they had 3 great-grandfathers, 17 grandfathers, 31 fathers, 48 sons, 14 grandsons and 3 cousins who also were celebrated.

C. THE KALLIKAK FAMILY

A more convincing experiment in human heredity than the foregoing, since it concerns the descendants of two mothers

and the same father, is furnished by the recently published history of the "Kallikak" family.[1]

During Revolutionary days, the first Martin Kallikak (the name is fictitious), who was descended from a long line of good English ancestry, took advantage of a feeble-minded girl. The result of their indulgence was a feeble-minded son who became the progenitor of 480 known descendants of whom 143 were distinctly feeble-minded, while most of the others fell below mediocrity without a single instance of exceptional ability.

"After the Revolutionary war, Martin married a Quaker girl of good ancestrty and settled down to live a respectable life after the traditions of his forefathers. From this legal union with a normal woman there have been 496 descendants. All of these except two have been of normal mentality and these two were not feeble-minded. . . . The fact that the descendants of both the normal and the feeble-minded mother have been traced and studied in every conceivable environment, and that the respective strains have always been true to type, tends to confirm the belief that heredity has been the determining factor in the formation of their respective characters."

It is to be noted that in this pedigree the maternal inheritance seems to give dominant character to the descendants. The same is also true of the Jonathan Edwards line, for Richard Edwards, the father of Jonathan Edwards, married twice, the first time to the brilliant but erratic Elizabeth Tuttle, whom he subsequently divorced, and the second time to Mary Talbot. The celebrated line of Jonathan Edwards, described by Winship, came through the first wife, while the descendants of Mary Talbot have been decidedly more mediocre,

[1] "The Kallikak Family," H. H. Goddard.

lacking the exceptional brilliance displayed by many of the descendants of Elizabeth Tuttle.

Other recent extensive studies of dysgenic lines include the "Nams," the "Hill Folk," the "Hickories," the "Pineys" of New Jersey, the "Ishmaels" of Indiana and the "Zeros" of Denmark.

These instances of human breeding show unmistakably that "blood counts" in human inheritance, even though the hereditary unit characters that lead to these general results have not yet been analyzed with the clearness that is possible in dealing with the characters of some animals and plants.

4. Moral and Mental Traits Behave like Physical Ones

In plants there is no question of moral and mental traits. In animals the rôle that these play is not easy to determine. When it comes to man the case is undoubtedly much more important and complex, since mental and moral characteristics have a large share in making man what he is. The brute acts according to his inherited organization; man is *urged* by his but *may* act according to a higher, moral law. There is, however, no fundamental scientific distinction that can be drawn between moral, mental, and physical traits, which undoubtedly are all equally subject to the laws of heredity.

For instance, as an illustration of the heritability of non-physical traits, in the Jukes pedigree three of the daughters of Max impressed their peculiar moral and mental characteristics in a distinctive way upon their offspring. To quote Davenport: "Thus in the same environment, the descendants of the illegitimate son of Ada are prevailingly *criminal;* the progeny of Belle are *sexually immoral*; and the offspring of Effie are *paupers*. The difference in the germplasm determines the difference in the prevailing trait." As Woods observes:

"The most interesting and even startling thing has been the ease with which heredity has been able to bear the brunt of explaining the general make-up of character."

5. The Character of Human Traits

Of the mental, moral, and physical traits that are heritable in man, some must be regarded as generally desirable, some as indifferent, and others as defects to be avoided if possible. In general the majority of human traits, those which together make up man as distinguished from other animals, do not particularly claim the attention because they are so universal. Some which stand out from the mass, such as the physical traits of eye-color and the color and character of hair, may be regarded as indifferent so far as the welfare of the individual is concerned, while others like skin color and certain racial features that characterize particular strains of "blood" may, under certain circumstances, work a social handicap upon their possessors according to the traditions of the community in which they appear.

A long list of desirable mental traits might easily be enumerated that seem in a general way to be subject to the laws of inheritance, although they have not yet undergone the careful analysis demanded by modern genetics which deals in separate characteristics rather than in lump inheritance.

The behavior of such mental traits cannot be tried out with lower animals and yet they are of the utmost importance in man.

Musical, literary, or artistic ability, for example, mathematical aptitude and inventive genius, as well as a cheerful disposition or a strong moral sense are probably all gifts that come in the germplasm. They may each be developed

by exercise or repressed by want of opportunity, nevertheless they are fundamentally germinal gifts.

A genius must be born of potential germplasm. There are no "self-made men" in the sense of rising above innate capacities by individual effort.

Each has within from his ancestry, the potentiality of whatever he becomes. No amount of faithful plodding application can compensate for a lack of the divine hereditary spark at the start.

6. Hereditary Defects

Undesirable hereditary traits are frequently defects due to the absence of some character. For instance, albinism, which occurs in several kinds of animals and also in man in one out of every 20,000 individuals (according to Elderton), is due to the absence of pigment in the skin, hair and eyes. Albinic individuals have poor eyesight because they are unable to stand strong light, being without protective pigment in the eyes. This peculiarity of albinism behaves as a recessive character both in man and in other mammals. An albinic individual may, therefore, marry a normal individual without fear of producing albino children, although the children of such a mating would carry heterozygous germplasm with respect to albinism, and in cousin marriages might subsequently produce some albino children.

Davenport, in his work on "Heredity in Relation to Eugenics," brings together a long catalogue of human hereditary defects, although in most instances they are extremely difficult to analyze accurately. This is true, first, because these defects so often depend probably upon a combination of determiners rather than upon a single one, and, second, because the available data are usually scattered and incomplete.

Deafness, for example, is a defect which is hereditary, though exactly to what degree, it is at present impossible to state. The following table taken from the extensive work of Fay (1898) upon "Marriage of the Deaf in America" gives some idea of the results of different matings lumped together statistically.

Condition of Parents	Percentage of Deaf Offspring
Both born deaf	25.9
One born deaf, one with acquired deafness	6.5
One born deaf, one normal	11.9
Both with acquired deafness	2.3
One with acquired deafness, one normal	2.2

That two parents born deaf do not produce more than 26 per cent of deaf children is probably due to the fact, first, that each parent is in all likelihood heterozygous for deafness and that, second, the same combination of factors which is the cause of the parental defect on either side of the pedigree does not happen to appear after segregation in the formation of the new individual.

If *A* and *B*, for example, represent two different dominant kinds of deafness, while *a* and *b* are the corresponding normal recessive allelomorphic traits for hearing, then, following Mendelian assortment, there is theoretically one chance in four that heterozygotic deaf parents (*Ab* and *aB*) may produce normal (*ab*) children.

Deafness will be produced in the offspring only when matings occur in which the proper factors are combined. Such an undesirable result is much more likely to happen if both parents come from the same, or related, hereditary strains than

if they are derived from families in no way connected by blood.

Herein lies the biological objection to cousin marriage which tends to bring together, and thus to perpetuate, like defects. Outcrossing, on the contrary, through the law of dominance, tends to conceal defects and to prevent their expression.

If the patent parental characters were all that reappeared in the offspring, the marriage of near kin would present fewer difficulties. It is the "skeleton in the closet" that makes trouble. Elderton gives a case of hæmophilia where the direct line was free from taint but collaterals showed the disease latent for six generations.

Inbreeding is often the result of proximity. Insular or isolated communities, slums in cities where those of one language herd together, or hovels in the backwoods where degenerates of a kind are kept in intimate association, as well as asylums of various sorts in which similar defectives are promiscuously housed under the same roof, are all potent agencies to insure human inbreeding.

Similarly, localities that have been devastated by migrations of the most effective blood, as, for example, parts of Ireland or many rural villages in New England, are frequently characterized by a population showing a large percentage of defectiveness. The able-bodied and ambitious go forth into the world to seek their fortunes, while the deficient in body or spirit are left behind where, under the spell of proximity, they perpetuate their deficiencies.

The part that improved transportation has played in mixing populations and in counteracting the effects of stagnation on human heredity, through inbreeding under the inertia of proximity, is very great. There were obviously geo-

graphic reasons for the well-known love story of Adam and Eve. Before the days of railroads and automobiles cousin-marriages were much more frequent than they are now.

When Mr. Ford removed the lid from Pandora's box by his well-known invention, there escaped facilities for intercommunication of untold consequence to eugenics.

Many cases of human defects, such as imbecility or insanity, are extremely difficult of analysis from the standpoint of heredity because, in the first place, the defective conditions descriptively included under these vague terms are made up of a multitude of diverse conditions each of which must have a different array of determiners, and, in the second place, because any one definite sort of insanity or imbecility may be conditioned by a variety of factors.

However, the difficulty of the problem is no reason for abandoning the attempt to reach its solution and to learn, if possible, "whence come our 300,000 insane and feeble-minded, our 160,000 blind or deaf, the 2,000,000 that are annually cared for by our hospitals and homes, our 80,000 prisoners and the thousands of criminals that are not in prison, and our 100,000 paupers in almshouses and out" (Davenport).

7. The Control of Defects

The method of possible control of human defects depends upon whether they are positive or negative, that is, dominant or recessive. In those cases where a given defect is due to a single determiner the Mendelian expectation for the possible offspring arising from various matings is indicated in the table on page 307 in which *D* stands for the defect and *d* for its absence.

If the defect is positive and in a duplex or homozygous condition in one parent, as in 1, 2, and 4, all the offspring

will possess it regardless of the germinal constitution of the other parent. In two cases only, namely, in 3 and 5, where the defective parent is heterozygous, is there any chance of unaffected offspring, and even in these cases the defect is

THE MENDELIAN EXPECTATION FOR DEFECTS

		IF THE DEFECT IS POSITIVE (dominant)	IF THE DEFECT IS NEGATIVE (recessive)
When both parents show the defect	1	$DD \times DD =$ all DD	$dd \times dd =$ all dd
	2	$DD \times Dd = \frac{1}{2}DD + \frac{1}{2}Dd$	
	3	$Dd \times Dd = \frac{1}{4}DD + \frac{1}{2}Dd + \frac{1}{4}dd$	
When one parent only shows the defect	4	$DD \times dd =$ all Dd	$dd \times DD =$ all Dd
	5	$Dd \times dd = \frac{1}{2}Dd + \frac{1}{2}dd$	$dd \times Dd = \frac{1}{2}Dd + \frac{1}{2}dd$
When neither parent shows the defect	6	$dd \times dd =$ all dd	$DD \times DD =$ all DD
	7		$Dd \times DD = \frac{1}{2}DD + \frac{1}{2}Dd$
	8		$Dd \times Dd = \frac{1}{4}DD + \frac{1}{2}Dd + \frac{1}{4}dd$

quite as likely to appear as not. It is obvious that the only way to rid germplasm of a dominant defect is by continued mating with recessive individuals. By this method it is possible in time to shake off the defect. When it once disappears in any individual, *it will never return* unless crossed back to a similar defective dominant strain.

In other words, such a recessive extracted from a heterozygous ancestry will breed just as true as a recessive which was pure from the start. In both instances there is an entire absence of the character in question, and it is clear that this character can thereafter never again reappear, since something cannot be derived from nothing.

On the other hand, if a defect is negative depending upon the absence of a normal dominant determiner, as is usually the case with defects, it behaves as a Mendelian recessive, that is, it is always apparent in individuals developing from the homozygously defective germplasm.

It is certain, for example, that an imbecile which has arisen from homozygous defective germplasm carries only the determiner for imbecility in his own germplasm, and when two

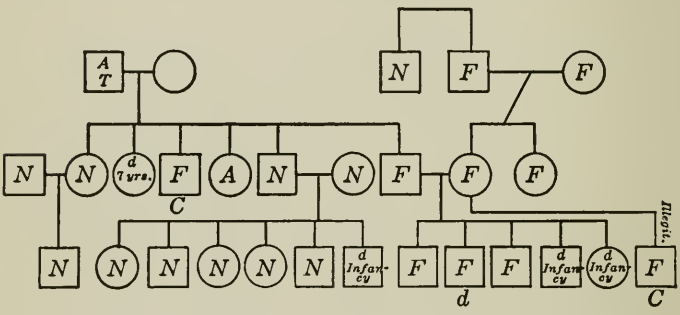

Fig. 92.—Pedigree chart illustrating the law that two defective parents have only defective offspring. *A*, alcoholic; *C*, criminalistic; *d*, died; *F*, feeble-minded; *N*, normal; *T*, tubercular. After Goddard.

such recessives mate, nothing but imbecile offspring can result, for recessives breed true. Nothing plus nothing equals nothing.

For practical purposes it is unimportant to know whether or not feeble-mindedness, or any similar defect, is Mendelian in behavior. The fact that it is hereditary is enough.

An illustration of this principle is given in the above pedigree (Fig. 92) furnished by Goddard, 1910. The result is quite different, however, when only one parent shows the defect. If the other parent is a normal homozygote, as in Case 4 of the accompanying table, all the offspring will be

normal in appearance but with the bar sinister of defectiveness in their germplasm, while if the parent is heterozygous (Case 5), one-half of the progeny will be defective.

Finally, when neither parent shows defectiveness, but one carries the defect as a heterozygote (Case 7), then there will be no defective children, while if both parents are heterozygous there is one chance in four that the offspring will be defective.

As a matter of fact, defectives usually mate with defectives for the simple reason that normal individuals ordinarily avoid them, so it comes about that streams of poor germplasm naturally flowing together tend toward the inbreeding of like defects.

Davenport [1] lays down the following general eugenic rules for the guidance of those who would produce offspring wisely: "If the negative character is, as in polydactylism and night-blindness, the *normal* character, then normals should marry normals, and they may be even cousins. If the negative character is *abnormal,* as imbecility and liability to respiratory diseases, then the marriage of two abnormals means probably all children abnormal; the marriage of two normals from defective strains means about one quarter of the children abnormal; but the marriage of a normal of the defective strain with one of a normal strain will probably lead to strong children. The worst possible marriage in this class of cases is that of cousins from the defective strain, especially if one or both have the defect. In a word, the consanguineous marriage of persons one or both of whom have the same undesirable defect, is highly unfit, and the marriage of even unrelated persons who both belong to strains containing the same undesirable defect is unfit. Weakness in any character-

[1] Davenport, Rep. of Amer. Breeders' Assoc., Vol. VI, 1910, p. 431.

istic must be mated with strength in that characteristic; and strength may be mated with weakness."

In short, the eugenical Cupid does not tell one so often whom to select for a partner as whom to avoid.

"Professor McCready, in his lectures at the College of Physicians and Surgeons, used to say his case records showed that for various reasons he had advised one or both parties against marriage some sixty-eight times; and that his records also showed that sixty-eight times the couples went almost straight to the altar." [1]

Thus it is that the knowledge which human beings possess concerning the laws of heredity is more frequently made use of theoretically than practically.

[1] Jour. Hered., November, 1919.

CHAPTER XV

HUMAN CONSERVATION

1. How Mankind May Be Improved

There are two fundamental biological ways to bring about human betterment, namely, by improving the individual and by improving the race. The first method consists in making the best of whatever heritage has been received by placing the individual in the most favorable environment and developing his capacities to the utmost through education and training. Under this head may be included such enterprises as improving sanitation, controlling disease, insuring health, safeguarding human life, banishing child-labor, lessening drudgery of all kinds, substituting something better for the slums, championing the weak, reforming penal institutions, maintaining charitable organizations, cultivating true temperance, dispelling ignorance and lengthening life. The second method consists in obtaining a better heritage with which to begin the life of the individual.

The first method is immediate and urgent for the present generation. The second method is concerned with ideals for the future, and consequently does not usually present so strong an appeal to the individual.

The first is the method of *euthenics,* or the science of learning to live well. The second is *eugenics,* which Galton defines as "the science of being well born." Every gain in eugenics, it need hardly be said, will make euthenics more effective but the reverse cannot be affirmed.

These two aspects of human betterment, however, are inseparable. Any hereditary characteristic must be regarded, not as an independent entity, but as *a reaction between the germplasm and its environment.* The biologist who disregards the fields of educational endeavor and environmental influence, is equally at fault with the sociologist who fails sufficiently to realize the fundamental importance of the germplasm.

Without euthenic opportunity the best of heritages can never fully come to its own. Without the eugenic foundation the best opportunity fails of accomplishment. The euthenic point of view, however, must not distract the attention now, for the present chapter is particularly concerned with the program of eugenics.

2. Human Assets and Liabilities

In an attempt to take account of human stock Dr. H. H. Laughlin, of the Eugenics Record Office, has made the following eugenical classification based on the manner in which families assemble in their offspring heritable traits which determine for their possessors (*a*) social adjustment and (*b*) special talent or defect.

I. Persons of genius;
II. Persons of special skill, intelligence, courage, unselfishness, enterprise or strength;
III. Persons constituting the great normal middle class, the "people";
IV. Socially inadequate persons.

The first three groups constitute those eugenically fit from sterling inheritance, who produce the socially valuable nine-tenths of humanity among civilized people, and in the last

group are the eugenically unfit from defective inheritance who produce the socially inadequate or the "submerged tenth" of humanity.

Among persons of genius Dr. Laughlin would include the 5000 persons most splendidly equipped by nature throughout historic times, as, for example, Aristotle in philosophy, Newton in science, Pasteur in medicine, Dante in poetry, Shakespeare in drama, and Cecil Rhodes in business. Reckoning that since civilization began there have been born and reared in civilized countries approximately thirty billion persons, the expectation of a genius is about 1 : 6,000,000.

In the second group are included the "natural and acknowledged leaders in all lines of human endeavor,—the *Who's Who* people." The incidence of these in the total population is possibly 1 : 6,000.

The third group, the "people," constitute nine-tenths of all, since the first two classes, although their influence is very great, are numerically negligible, while the fourth group is made up of the residue or the socially inadequate, namely, (1) feeble-minded; (2) pauper; (3) inebriate; (4) criminalistic; (5) epileptic; (6) insane; (7) asthenic or weak; (8) diathetic, or predisposed to disease; (9) deformed; (10) cacæsthenic, that is, with defective sense organs.

Laughlin concludes: "The task of eugenics is (1) to encourage fit and fertile matings among those persons most richly endowed by nature and (2) to devise practicable means for cutting off the inheritance lines of persons of naturally meager or defective inheritance."

3. More Facts Needed

Since the point of attack in human heredity must be largely statistical, it is of the first importance to collect more facts.

Our actual knowledge is confused with a mass of tradition and opinion, much of which rests upon questionable foundations. The great present need is to learn more facts; to sift the truth from error in what is already known; and to reduce all these data to workable scientific form. Much progress is being made in this direction, owing to the impetus given by the revival of Mendel's illuminating work, but as yet the science of eugenics is in its infancy.

Eugenics, being a biological science, its truths cannot be arrived at by arbitration and discussion. No doubt the entire eugenic movement has suffered much at the hands of its over-enthusiastic friends since there is a wide difference between eugenic zeal and eugenic knowledge and wisdom.

"If there is one thing to be deprecated little less than ignorance or indifference," says Sir John MacDonald, "it is science in a hurry,—eagerness to go to market with one's crops before they are fully ripe." This is particularly true in the field of eugenics.

The most systematic and effective attempt in this country to collect reliable data concerning heredity in man has been initiated under the leadership of Dr. C. B. Davenport in connection with what is now the Department of Genetics of the Carnegie Institution of Washington which began in 1910 as the Eugenics Record Office, with a staff of expert field and office workers and an adequate equipment for the preservation of records, at Cold Spring Harbor, Long Island, New York, under Dr. H. H. Laughlin as superintendent. "The main work of this office is investigation into the laws of inheritance of traits in human beings and their application to eugenics." Already a considerable number of valuable publications, based upon data obtained, have been issued from the Eugenics Record Office.

The Volta Bureau, founded nearly fifty years ago in Washington by Dr. Alexander Graham Bell, is collecting data with reference to deafness and has to date systematically arranged particulars concerning the history of over 20,000 individuals. In England the Galton Laboratory for Eugenics, founded in 1905, is systematically collecting facts about human pedigrees and publishing the results in a compendious "Treasury of Human Inheritance."

Besides these special bureaus of investigation, innumerable facts throughout the world about the inheritance of particular traits are everywhere being incidentally brought together and made available in various institutions and asylums immediately concerned with the care of defectives of different types. It is in connection with such institutions for defectives in the United States that much of the most successful "field work" is being accomplished.

Among periodical publications in the United States devoted especially to this field, should be mentioned "Eugenics" and "Eugenical News," the official organs respectively of *The American Eugenics Society* and *The Eugenics Research Association.*

4. Further Application of What We Know Necessary

Human performance always lags behind human knowledge. Many persons who are fully aware of the right procedure do not put their knowledge into practice. It follows, therefore, that any program of eugenics which does not grip the imagination of the common people in such a way as to become an effective part of their very lives is bound to remain largely an academic affair for Utopians to quarrel and theorize over.

Important as the preliminary step is of collecting facts and

working out an analysis and interpretation of them, it must be followed by a convincing campaign of education, and not until a sufficient barrage of preparatory education has been laid down will it be possible to go over the top with effective legislation in the application of eugenic principles.

The lives of the unborn do not force themselves upon the average man or woman with the same insistency as lives already begun. In the midst of the overwhelming demands of the present, the appeal of posterity for better blood is vague and remote. If every individual regarded the germplasm he carries as a sacred trust, then it would be the part of an awakened eugenic conscience to restrain that germplasm when it is known to be defective or, when it is not defective, to hand it on to posterity with at least as much foresight as is exercised in breeding domestic animals and cultivated plants.

It is a far more solemn responsibility eugenically to *give* than to *take* human life.

The eugenic conscience is in need of development, and only when it shall have become thoroughly aroused in the rank and file of society as well as among the leaders, can a permanent and increasing betterment of mankind be expected.

5. Restriction of Undesirable Germplasm

A negative way to bring about better blood in the world is to follow the clarion call of Davenport and "dry up the streams that feed the torrent of defective and degenerate protoplasm."

The education of the feeble-minded, the cure of the insane and the reform of the criminal are all euthenic not eugenic means of relief. Some idea of the extent of the drag of the "submerged tenth" upon human society may be gained from the following table, the data for which are derived from the

U. S. census.[1] Similar figures of a more recent date would no doubt point the same moral.

STATE INSTITUTIONS FOR DEFECTIVE, DEPENDENT AND DELINQUENT CLASSES

Institutions for	No. of Inmates Jan. 1, 1916	No. of Institutions	Expenditures for Maintenance and Operation in 1915
1. Insane	199,340	147	$36,312,662.20
2. Criminalistic	95,985	170	21,244,892.00
3. Dependent	45,373	84	9,675,932.37
4. Tuberculous	7,187	45	3,539,454.95
5. Feeble-minded	19,298	27	3,341,442.85
6. Deaf	6,826	33	1,893,490.09
7. Epileptic	6,097	9	1,345,821.57
8. Feeble-minded and epileptic	6,984	9	1,285,500.05
9. Blind	3,118	28	1,066,973.14
10. Blind and deaf	2,233	12	615,468.41
11. Inebriate	615	3	232,080.62
12. Deformed	601	4	206,747.23
13. Criminalistic and dependent	814	1	105,705.86
14. Feeble-minded, blind and deaf	191	1	67,051.73
15. Blind, deaf and dependent	215	1	59,649.67
16. Leprous	114	2	56,118.19
TOTAL	394,991	576	$81,048,990.93

The burden of the three undesirable D's, "defectives, dependents and delinquents," upon human society is by no means entirely represented in the dollar-column of this table. Each individual recorded is a human being, the member of some family and community, which must be more or less directly borne down by the unfortunate one. Moreover, the unfortunates who are in institutions are but a small percentage of the total number in the population who are not in institutions. It should be remembered that although heredity plays an important part in such life-tragedies it is not entirely to blame for these depressing data.

[1] Statistical Directory of State Institutions for the Defective, Dependent and Delinquent Classes. Laughlin. Washington, 1919.

The restriction of undesirable additions to our human stock may be partially accomplished, at least in America, by employing the following agencies: control of immigration; more discriminating marriage laws; a quickened eugenic conscience; sexual segregation of defectives; and finally, drastic measures of asexualization when necessary. Providing for the eugenic elimination of defectives, or the prevention of their conception, is as truly a civic duty as administering charity to them after they are born.

A. CONTROL OF IMMIGRATION

The enforcement of proper immigration laws tends to debar from the United States not only many undesirable individuals, but also, incidentally, to keep out much potentially bad germplasm which, if admitted, might play havoc with future generations.

It is not enough to lift the eyelid of a prospective parent of American citizens to discover whether he has some kind of an eye-disease or to count the contents of his purse to see if he can pay his own way. The official ought to know whether eye-disease runs in the immigrant's family and whether he comes from a race of people which, through chronic shiftlessness or lack of initiative, have always carried light purses.

In selecting horses for a stock-farm an expert horseman might rely to a considerable extent upon his judgment of horseflesh based upon inspection alone, but the wise breeder does more than take the chances of an ordinary horse-trader. He wants to be assured of the *pedigree* of his prospective stock. It is to be hoped that the time will come when we, as a nation, will rise above the hazardous methods of the horse-trader in selecting from the foreign applicants who knock

at our portals, and that we will exercise a more fundamental discrimination than such a haphazard method affords, by demanding a knowledge of the germplasm of these candidates for citizenship, as displayed in their pedigrees.

The United States Department of Agriculture has for many years had field agents scouring every land for desirable animals and plants to introduce into this country, as well as stringent laws to prevent the importation of dangerous weeds, parasites, and organisms of various kinds. The devastation wrought by the admission to this country of such insects, for example, as the gipsy moth, Japanese beetle, and Mediterranean fruit-fly is common knowledge. Is the inspection and supervision of human blood less important?

During the year of 1908, for example, 65 idiots, 121 feeble-minded, 184 insane, 3741 paupers, 2900 individuals having contagious diseases, 53 tuberculous individuals, 136 criminals, and 124 prostitutes were caught in the sieve at Ellis Island alone and turned back from this country by the immigration officials in spite of the fact that an average of only 8 cents a head was expended upon inspection.

These individuals probably were the bearers of very little germplasm that we are nationally not better off without.

Eugenically, the weak point in the present application of immigration laws is that criteria for exclusion are phenotypic in nature rather than genotypic, and consequently much bad germplasm comes through our gates hidden from the view of inspectors because the bearers are heterozygous, wearing a cloak of desirability over undesirable traits.

B. MORE DISCRIMINATING MARRIAGE LAWS

Every people, including even the more primitive races, have customs or make laws that tend to regulate marriage. Of these,

the laws which relate to the eugenic aspect of marriage are the only ones that concern us in this connection. "Marriage," says Davenport, "can be looked at from many points of view. In novels as the climax of human courtship; in law largely as two lines of property descent; in society, as fixing a certain status; but in eugenics, which considers its biological aspect, marriage is an experiment in breeding."

Certain of the United States have laws forbidding the marriage of epileptics, habitual drunkards, paupers, idiots, the insane, feeble-minded, and those afflicted with venereal diseases. It would be well if such laws were not only more uniform and widespread, but also more rigidly enforced.

The fact that much marriage taboo already exists regardless of laws, which effectually hinders or prevents certain kinds of undesirable matings, forms a basis of hope for more efficient future control.

It is quite true that marriage laws in themselves do not necessarily control human reproduction, for illegitimacy is a factor that must always be reckoned with; nevertheless such laws do have an important influence in regulating marriage and consequent reproduction. Incidentally it may be pointed out that in a biological sense there is no such thing as an "illegitimate" child. Only parents can be illegitimate.

Marriage laws may, however, sometimes bring about a deplorable result eugenically, as in the case of forced marriage of sexual offenders in order to legalize the offense and "save the woman's honor." To compel, under the guise of legality, two defective streams of germplasm to combine repeatedly and thereby result in defective offspring just because the unfortunate event happened once illegitimately, is fundamentally a mistake. Darwin says: "Except in the case of man himself

hardly anyone is so ignorant as to allow his worst animals to breed."

C. AN EDUCATED SENTIMENT

A far more effective means of restricting bad germplasm than by placing elaborate marriage laws upon our statute-books is to educate public sentiment and to foster a popular eugenic conscience, in the absence of which the safeguards of the law must forever be largely without avail, since our best hope lies not in compulsion but in voluntary effort.

Such a sentiment already generally exists to a large extent with respect to incest, and the marriage of persons as noticeably defective as idiots or those afflicted with insanity, and also in America with respect to miscegenation, but a cautious and intelligent examination of the more obscure defective traits, exhibited in the somatoplasms of the various members of families in question, is largely an ideal of the future. Under existing conditions non-eugenic considerations such as wealth or social position often enter into the preliminary negotiations of a marriage alliance, but an equally unromantic caution with reference to the physical, moral, and mental characters that make up the biological heritage of contracting parties is less usual.

It was William Penn who said "Marry only for love but be sure that thou lovest what is lovely."

The scientific attitude is not necessarily opposed to the romantic way of looking at things. If the bandage across the eyes of blind Cupid is allowed to slip a little in so important and far-reaching an operation as "falling in love" it is perhaps just as well. The dialogue in "Two Gentlemen of Verona" between Julia and Lucetta is quite to the point where the eager and curious Julia says to her maid,—

"But say, Lucetta, now we are alone,
Woulds't thou counsel me to fall in love?"

and the canny Lucetta makes reply,—

"Aye, Madam, so you *stumble not unheedfully.*"

This advice is simply "organized common sense," and romance, which dispenses with this balance-wheel, although it may be entertaining and always exciting at first, is sure to be disappointing in the end. Marriages may be "made in heaven," but, as a matter of fact, children are born and have to be brought up on earth, and there is nothing particularly romantic in defective children who might better never have been born.

It follows without saying that it will be much easier to stamp out bad germplasm when an educated sentiment becomes common among all people everywhere.

D. SEGREGATION OF DEFECTIVES

Persons with hereditary defects, such as epileptics, idiots, and certain incorrigible criminals, who become wards of the state, should be segregated or confined in comfort so that their germplasm may not escape to furnish additional burdens upon society. "We have become so used to crime, disease and degeneracy that we take them for necessary evils. That they were, in the world's ignorance, is granted. That they must remain so, is denied" (Davenport).

"The great horde of defectives once in the world have the right to live and enjoy as best they may whatever freedom is compatible with the lives and freedom of other members of society," says Kellicott, "but society has a right to protect itself against repetitions of hereditary blunders."

There is one grave danger connected with the administra-

tion of our humane and commendable philanthropies for the unfortunate, since it frequently happens that defectives are kept in institutions until they are sexually mature or are partly self-supporting, when they are liberated only to add to the burden of society by reproducing their like.

Furthermore, if defectives of the same sort are collected together in the same institutions, unless sexual segregation is strictly maintained, they may by the very circumstance of proximity tend to reproduce their kind just as defectives in any isolated community tend to multiply. There is much misplaced philanthropy that is euthenic but not eugenic. The temporary troubles of the individual may be alleviated only to make possible a future addition to the burden of society.

Justice Oliver Wendell Holmes put the whole matter in a nutshell when he said: "Three generations of imbeciles are enough."

The interesting case of *cretinism* which is unusually common in the valley of Aosta in northern Italy, is cited by David Starr Jordan to prove the wisdom of the sexual segregation of defectives. Cretinism is an hereditary defect connected with an abnormal development of the thyroid gland that results in a peculiar form of idiocy ordinarily associated with goitre. "In the city of Aosta the goitrous *cretin* has been for centuries an object of charity. The idiot has received generous support, while the poor farmer or laborer with brains and no goitre has had the severest of struggles. In the competition of life a premium has thus been placed on imbecility and disease. The *cretin* has mated with *cretin,* the goitre with goitre, and charity and religion have presided over the union. The result is that idiocy is multiplied and intensified. The *cretin* of Aosta has been developed as a new species of man. In fair weather the roads about the city are lined with these

awful paupers—human beings with less intelligence than a goose, with less decency than the pig."

Whymper, writing in 1880, further observes: "It is strange that self-interest does not lead the natives of Aosta to place their *cretins* under such restrictions as would prevent their illicit intercourse; and it is still more surprising to find the Catholic Church actually legalizing their marriage. There is something horribly grotesque in the idea of solemnizing the union of a brace of idiots, and, since it is well known that the disease is hereditary and develops in successive generations the fact that such marriages are sanctioned is scandalous and infamous."

Since 1890 the *cretins* have been sexually segregated, and in 1910 Jordan reported that they were nearly all gone.

E. DRASTIC MEASURES

A fifth method of restricting undesirable germplasm in the case of confirmed criminals, idiots, imbeciles, and rapists may be mentioned, namely, the extreme treatment of surgically preventing possible parenthood. There are various ways in which this may be accomplished. *Vasectomy* is a minor operation confined to the male which occupies only a few moments and requires at most only the application of a local anæsthetic. There are probably no disturbing or even inconvenient after-effects from this operation. It consists of removing a small section of each sperm duct and is entirely effectual in preventing subsequent parenthood.

In the female the corresponding operation of *salpingectomy* consists in removing a portion of each Fallopian tube, and is much more severe but not impracticable or dangerous.

According to Laughlin who has carefully collected data on the subject, in 20 of the 24 states which have enacted

eugenical sterilization statutes the law is still (1929) on the statute books, unattacked by courts and so still available for use. From the beginning of legal sterilization in the United States in 1907 until January 1st, 1928, a total of 8515 cacogenic persons have been made sexually sterile under the several statutes.

Laughlin goes on to point out that "the nature of administrative machinery, which will work and which will fail, is, from the experiments already made, fairly well known, so that if the principle of eugenical sterilization has public support, practically any state legislature can, if it chooses, enact a well-functioning law."

In 1927 the Supreme Court of the United States upheld the constitutionality of the Virginia sterilization law which had been written on a purely eugenical basis, eliminating all elements of punishment. This decision marked the turning point in twenty years of experimental legislation. Now any state can, if it desires, enact a sterilization statute, based on purely eugenical motives, which will be upheld by the courts. The principal task of the states in using eugenical sterilization is to make sure that their administrative machinery will sterilize only indivdiuals who, by modern pedigree analysis, are demonstrated beyond reasonable doubt to carry hereditary defectiveness or degeneracy.

Eugenical sterilization may be said to have passed the experimental stage and it is now a conservative instrument of the State to be employed in the fight against hereditary degeneracy.

The province of Alberta, Canada, enacted a sterilization statute in 1928; the canton of Vaud, Switzerland, provided for legal sterilization in 1928, and Denmark passed a national sterilization act in 1929.

6. The Conservation of Desirable Germplasm

The eugenic ideal may be approached not only negatively by the restriction of undesirable germplasm, but also positively by the conservation of desirable germplasm.

Various ways in which this improvement of society may be brought about are:

A. BY ENLARGING INDIVIDUAL OPPORTUNITY

Much good human germplasm goes to waste through ineffectiveness on account of unfavorable environment or lack of a suitable opportunity to develop.

Every agency which contributes toward increasing the opportunity of the individual to attain to a better development of his latent possibilities is in harmony with a thoroughly positive eugenic practice. Thus better schools, better homes, better living conditions, in short, all euthenic endeavor, directly serves the eugenic ideal by making the best out of whatever germinal equipment is present in man.

B. BY PREVENTING GERMINAL WASTE

Much good protoplasm fails to find expression in the form of offspring because one or the other of possible parents is cut off either by preventable death or by social hindrances. To avoid such calamities is a part of the positive program of eugenics.

a. Preventable Death

War, from the eugenic point of view, is the height of folly, since presumably the brave and the physically fit march away to fight, while in general the unqualified stay at home to re-

produce the next generation. When a soldier dies on the battlefield or in the hospital, it is not alone a brave man who is cut off, but it is the termination of a probably desirable strain of germplasm.

David Starr Jordan has presented this matter very clearly. He points out that the depressed and stupid "man with a hoe" among the European peasantry is not the result of centuries of oppression, as he has been pictured, but rather the dull progeny resulting from generations of the unfit who were left behind when the fit went off to war never to return.

Benjamin Franklin, with characteristic wisdom, sums up the situation in the following epigram: "Wars are not paid for in war time; the bill comes later."

b. Social Hindrances

There are many conditions of modern society which act non-eugenically.

For instance, the increasing demands of professional life prolong the period necessary for preparation, which, together with the "high cost of living," and the *cost of high living,* tend toward late marriage. In this way much of the best germplasm is very often withheld from circulation until it is too late to be effective in providing for the succeeding generation.

Certain occupations such as school-teaching and nursing by women are filled by the best blood obtainable, yet this blood is often denied a direct part in molding posterity, since marriage is frequently either forbidden or regarded as a serious handicap in such lines of work. Advertisements concerning "unincumbered help" and "childless apartments" tell their own deplorable tale.

One of the darkest features of the dark ages from a eugenic

standpoint was the enforced celibacy of the priesthood, since this resulted, as a rule, in withdrawing into monasteries and nunneries much of the best blood of the times, and this uneugenic custom still obtains in many quarters to-day.

c. By subsidizing the fit

It is possible that if some of the philanthropic endeavor now directed toward alleviating the condition of the unfit should be directed to *enlarging the opportunity of the fit,* greater good would result in the end. This was the very wise policy of Andrew Carnegie in arranging his colossal philanthropies.

In breeding animals and plants the most notable advances have been made by isolating and developing the best, rather than by attempting to raise the standard of mediocrity through the elimination of the worst.

One leader is worth a score of followers in any community, and the science of genetics surely gives to educators the hint that it is wiser to cultivate the exceptional pupil, who is often left to take care of himself, than to expend all the energies of the instructor in forcing the indifferent or ordinary one up to passage of a standard. The campaign for human betterment in the long run *must do more than avoid mistakes.* It must become aggressive and take advantage of those human mutations or combinations of traits which appear in the exceptionally endowed.

Bateson, however, with his usual caution voices the warning, "It is evident that while the elimination of the hopelessly unfit is a reasonable and prudent policy for society to adopt, any attempt to distinguish certain strains as superior and to give special encouragement to them would probably fail to accomplish the object proposed."

7. Who Shall Sit in Judgment?

In the practical application of a program of eugenics there are many difficulties, for who is qualified to sit in judgment and separate the fit from the unfit?

There are certain strongly marked characteristics in mankind which are plainly good or bad, but the principle of the independence of hereditary characters demonstrates that no person is wholly good or wholly bad. Shall we then throw away the whole bundle of sticks because it contains a few poor or crooked ones? Is it wise to burn the barn in order to kill the rats?

The list of weakling babies, for instance, who were apparently physically unfit and hardly worth raising upon first judgment, but who afterwards became powerful factors in the world's progress, is a notable one and includes the names of Calvin, Newton, Heine, Voltaire, Herbert Spencer, Roosevelt, and Robert Louis Stevenson.

Dr. C. V. Chapin, whose national fame and wide experience as a civic health officer gives weight to his opinion, recently said with reference to the eugenic regulation of marriage by physician's certificate: "The causes of heredity are many and very conflicting. The subject is a difficult one, and I for one would hesitate to say, in a great many cases where I have a pretty good knowledge of the family, where marriage would, or would not, be desirable."

Desirability and undesirability must always be regarded as relative terms more or less undefinable. In attempting to set a limit, it makes a great difference whether the interested party holds to a puritan or a cavalier standard. The concept of what is "best" varies with the times and the people involved. To show how far human judgment may err as well as how

radically human opinion changes, there were in England, as recently as 1819, 233 crimes punishable by death according to law.

One needs only to recall the days of the Spanish Inquisition or of the Salem witchcraft persecution to realize what fearful blunders human judgment is capable of, but it is unlikely that the world will ever see another great religious inquisition, or that in applying to man the newly found laws of heredity there will ever be undertaken an equally deplorable eugenic inquisition.

It is quite apparent, finally, that although great caution and broadness of vision must be exercised in bringing about the fulfillment of the highest eugenic ideals, nevertheless in this direction lies the future path of human achievement.

8. Eugenics, not "Bluegenics"

Eugenics has been called the "dismal science" by romantic people who chafe under the restrictions of common sense, and by conscientious individuals who are depressed by the appalling hereditary blunders made by mankind, but, as a matter of fact, eugenics presents the brightest hope for the future of humanity. Some of the unattractiveness of the eugenical program lies in the fact that it calls for results in the distant future in which there can be little or no personal participation, and often at the expense of present-day comforts. It is a lofty ideal of altruism and patriotism, which in the ringing words of Major Leonard Darwin, is *"an ideal to be followed like a flag in battle without thought of personal gain."*

9. The Moral

Race-preservation, not self-preservation, is the first law of nature. Because the laws of heredity work relentlessly within

predetermined limits is no reason for branding eugenics with the mark of a fatalistic philosophy that would avoid personal responsibility. The Florida orange-grower who uses his intelligence and plants frost-resisting varieties to replace those overtaken by frost does not blame fate for his former losses. It is never fatalistic to seek to find out the true determining causes of a disaster and to apply the obvious remedy. As Osborn has said: "To know the worst as well as the best in heredity; to preserve and select the best, these are the most essential forces in the future evolution of human society."

Our hereditary endowment may be something given us without our consent and connivance, while the accident of our birth may determine very largely the environment in which we must work out our salvation, but *there lies a sleeping giant of possibility in everyone,* and, whether we have one talent or five or ten, the individual response we make is our own and we alone are responsible for it.

Finally, to quote the wise words of Huxley,—"To learn what is true in order to do what is right is the summing up of the whole duty of man, for all who are not able to satisfy their mental hunger with the east wind of authority."

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